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THE IMPACTS OF PRESCRIBED BURNING AND MECHANICAL THINNING ON
INSECT COMMUNITIES IN THE ARKANSAS OZARKS

By

Aaron P. Tormanen

Submitted to the Faculty of the Graduate College of
Arkansas Tech University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE IN FISHERIES AND WILDLIFE SCIENCE
August 2020

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Abstract

Insects are important in woodland ecosystems due to their role as pollinators and as prey for bats. My research investigated the relationships between forest management, vegetation, and insects in the Ozark National Forest in Arkansas. I selected 30 stands burned at varying frequencies in the last 12 years. Twelve of these stands were burned and mechanically thinned, 12 were only burned, and 6 were untreated. I deployed blacklight traps and malaise traps in each stand monthly from mid-March to mid-November 2019. Over 42,391 insects were collected, and Lepidoptera was the most abundant order. Insects were dried, weighed, and identified for diversity metrics. I used multi-model selection and AICc to find the top models from a series of linear mixed effects models to determine the best forest management strategies for bat prey and the best vegetation habitat for pollinators. Total biomass of nocturnal, aerial insects was lower in thinned stands despite thinned stands having more ground vegetation. However, it is unclear if it is the removal of Lepidoptera tree hosts or changes to bat foraging activity that drove this relationship. Stands burned at high frequencies had a higher abundance of Coleoptera and more ground vegetation that is important insect habitat. The intermediate disturbance hypothesis is not a universal ecological rule and was not supported with regards to Lepidoptera diversity and burn frequency. However, more research needs to be done to determine if there is an intermediate tree density that balances the benefits to Lepidoptera bat-prey and Hymenoptera pollinators.

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CHAPTER 1:

BAT PREY RESPONSES TO PRESCRIBED BURNS AND MECHANICAL THINNING

Introduction

Burn History of the Ozarks

Arkansas has a long history of timber management, with intentional burning and cutting dating back to the Hopewell Native Americans in the first century (McGimsey 1969), and these anthropogenic changes continued with the arrival of the Quapaw (Baird 1980). The Ozark National Forest is managed forest land in the Boston Mountains of the Ozark Mountain region in Arkansas. The Ozark Mountains were historically recorded as consisting of a multitude of ecotones including prairie, savannas, woodlands, and forests prior to European settlement (Schoolcraft 1821). Tree-ring analyses suggest that fire frequency abruptly declined coinciding with European settlement of the region (Cutter and Guyette 1994, Guyette and Cutter 1997, Guyette et al. 2006). This is largely attributed to intensive logging and farming practices by settlers that decreased fuel loads and prevented fires from igniting and spreading (Cutter and Guyette 1994). However, some tree-ring analyses specific to the Lower Boston Mountains show an increase in fire frequency with the increase in human population density that came with the arrival of European settlers (Guyette and Spetich 2003, Engbring et al. 2008).

Similar to how forests are managed today, Native Americans in the Mid-South burned forests frequently for hunting, improving wildlife habitat, warfare, clearing land, and even reducing fuel loads to prevent more catastrophic fires (Hudson 1976, Elliott et al. 1999). European settlers first had contact with Native Americans in the Arkansas

River Valley in the 1500s (Whayne 1995). These settlers conducted burnings of their own in the Ozarks starting in the early 1800s with timber harvests that often preceded fires peaking in the early 1900s (Bass 1981). Suppression of forest fires increased in the early 1900s, with efforts to suppress fires in the area that is now the Ozark National Forest being largely futile (Bruner 1930). Fire suppression efforts were eventually successful in the Ozark National Forest in the 1930s, with the message of the perceived benefits of fire prevention spreading to rural areas (Strausberg and Hough 1997). This fire suppression is believed to be responsible for transforming open prairie, savanna, and woodland habitat to dense forests in the central hardwood forest region (Beilmann and Brenner 1951, Komarek 1974, Brose et al. 2001). General Land Office records indicate that the tree density in the Ozarks was approximately 94–188 trees per ha before European settlement, compared to approximately 741–2471 trees per ha today (Anderson et al. 2003). With the presence of humans in North America dating back thousands of years and the lack of data on burn frequencies before these times, it is difficult to fully understand the natural frequency of fires in the Ozarks and the role it played ecologically.

In the Mid-South, there are approximately 1–5 natural lightning ignitions per year, per 400,000 ha (Schroeder and Buck 1970), which is approximately the size of the Ozark National Forest. Fires that were the result of lightning may have been more capable of spreading and burning large areas prior to the arrival of humans due to the lack of forest fragmentation (Duncan and Schmalzer 2004, Salvati et al. 2015), but it is unknown how frequently large wildfires occurred and how effective they were at maintaining woodland and savanna habitat. Despite these natural wildfires caused by lightning playing an ecological role prior to the arrival of humans, these lightning-induced

fires were likely rare due to specific conditions needed that includes low moisture and precipitation, which is not the case during lightning storms with heavy rainfall (Nash and Johnson 1996, Rorig and Ferguson 2002).

Burning, Thinning, and Lepidoptera

In order to return the Ozarks to the low tree densities that are characteristic of woodlands, 2 primary methods of tree removal are used: prescribed burning and mechanical timber thinning (McMurry et al. 2007, Kinkead 2013). Removing the tree canopy and ground litter through burning is beneficial to the understory and ground vegetation by removing barriers that prevent sunlight from reaching the forest floor (Wang et al. 2005). This process of improving vegetation structure may also benefit insects, such as moths and butterflies (Order: Lepidoptera), by improving habitat and forage, as plant community structure is the main driver of Lepidoptera abundance (White 1974, Thompson and Price 1977, Thompson 1978, Dempster 1983, Summerville and Crist 2008, Shuey et al. 2012). However, burning alone may not turn dense forests into woodlands. In the Ozark Highlands, prescribed burning alone has been unsuccessful in decreasing the canopy cover enough to fit the definition of a savanna or woodland, or in allowing a sufficient amount of sunlight to reach the forest floor (Dey and Hartman 2005, McMurry et al. 2007, Kinkead 2013). Sites that have been burned, but not thinned, also tend to have a greater number of oak (*Quercus*) competitors compared to sites that were burned and thinned (Kinkead 2013).

Prescribed burning following timber harvest was first proposed as a forest management strategy for oaks by Hannah (1987). The combination of burning and thinning significantly increases understory vegetation diversity (Abella et al. 2001,

McMurry et al. 2007, Kinkead 2013). In a Virginia oak forest, prescribed burning 2–4 years after a shelterwood harvest allowed hickory (*Carya*) and oak species to outcompete shade-tolerant red maple (*Acer rubrum*) and yellow-poplar (*Liriodendron tulipifera*) during regeneration when compared to shelterwood harvested stands that were not burned (Brose and Van Lear 1998, Brose et al. 1999). Prescribed burning in shortleaf pine (*Pinus echinata*) forests in the southeastern United States has increased the proportion of shortleaf pine seedlings in the understory compared to competing tree species (Williams 1998, Dey and Hartman 2005). Despite some evidence that burning and mechanically thinning a stand may be better at restoring understory vegetation and regenerating desired tree species than thinning alone, few studies have compared burned and harvested stands to stands that received only burning.

Despite the potential ecological benefits of burning at frequent intervals, burning too frequently may have detrimental effects to some biological communities. Prescribed burning of an Illinois oak forest every year for 17 years resulted in increasing overall understory vegetation diversity, but also eliminated native shrub species that could be important habitat and forage for native invertebrates and wildlife (Bowles et al. 2007). Similarly, in the Florida sandhills, more frequent burning has been associated with a lower biomass of Lepidoptera, and tree stands that were burned every 3–5 years had greater heterogeneity of tree species compared to stands that were burned every 1–2 years or every 8 years or greater (Armitage and Ober 2012). However, in areas of the Talladega National Forest in Alabama where bat activity was acoustically monitored, insect diversity and abundance (most of which were Lepidoptera and Coleoptera) was greatest with intermediate burn frequencies (once every 4–8 years) and lowest with high burn

frequencies (once every 0–4 years) (Dover and Payne 2018). These studies suggest that intermediate fire frequency could be more beneficial to vegetation structure and insect abundance and diversity than less frequent or overly frequent disturbance regimes. This is consistent with the intermediate disturbance hypothesis, which suggests that intermediate frequencies and intensities of disturbance result in the greatest biodiversity (Connell 1978, Sousa 1979).

The relationship between disturbance and Lepidoptera is complicated and influenced by many factors. Unlike unburned areas, recently burned areas often lack larval Lepidoptera (Sileshi and Mafongoya 2006), presumably due to direct fire-related mortality, as well as adult Lepidoptera that fly into nighttime fires and burn (Gerson and Kelsey 1997). Despite this short-term response, prescribed burning and mechanical thinning can improve understory vegetation diversity in the long-term by reducing canopy tree density and promoting regeneration (Brose and Van Lear 1998). This may be beneficial for Lepidoptera habitat, as Lepidoptera species richness is associated with the presence of grasses and herbaceous vegetation (Hammond and Miller 1998). However, this reduction in tree density results in a temporary reduction in canopy trees, which provide important habitats for larval Lepidoptera (Butler and Strazanac 2000, Tallamy and Shropshire 2009). Oaks in particular have high larval Lepidoptera species diversity and density (Maier and Davis 1989, Wagner et al. 2003), but some species, such as the imperial moth (*Eacles imperialis*), use pines as hosts (Goldstein 2010, Spencer 2014).

Mechanical thinning could be a potential management strategy for Lepidoptera conservation by representing an intermediate intensity of disturbance compared to high intensity clearcutting or shelterwood harvests. Cleared areas with no trees are known to

have the lowest Lepidoptera abundance and species diversity compared to tree stands (Burford et al. 1999), and both clearcutting and shelterwood harvest can lower the species richness and abundance of Lepidoptera (Summerville 2011, Summerville et al. 2013). However, despite Lepidoptera abundance decreasing when more trees were removed, Lepidoptera species richness peaked in stands thinned with 30% of trees removed compared to unthinned stands and stands with 50% and 100% of trees removed in a New Brunswick red spruce (*Picea rubens*) forest (Thomas 2002). A balance may be needed in which thinning sufficiently increases the number of Lepidoptera species present while still providing enough larval host trees to allow for a diverse and abundant Lepidoptera community to thrive.

Although the presence of canopy trees may increase the overall abundance of Lepidoptera, it may not be ecologically beneficial if the dominant species is a pest species that defoliates host trees and outcompetes other Lepidoptera species, potentially lowering native Lepidoptera species diversity. In the taiga along the Finnish-Russian border, pest-damage caused by the European pine looper (*Bupalus piniaria*) was greater on the Russian side of the border where pine stands were not mechanically thinned compared to pine stands on the Finnish side of the border that were mechanically thinned (Veteli et al. 2006). In an Indiana oak forest, clearcutting and shelterwood harvests reduced the abundance of the eastern tent caterpillar (*Malacosoma americanum*), but resulted in the colonization of Lepidoptera row crop pests, including the European corn borer (*Ostrinia nubilalis*), gold triangle (*Hypsopygia costalis*), and the corn earworm (*Helicoverpa zea*) (Summerville et al. 2013). Determining the relationship between thinning and Lepidoptera pests is applicable to the Ozark Mountains region because the

majority of the Ozarks in Arkansas are susceptible to gypsy moth (*Lymantria dispar dispar*) infestation (Liebhold et al. 2004).

Chiroptera and Lepidoptera

The diet of bats (Order: Chiroptera) is made up of multiple insect orders including beetles (Order: Coleoptera) and flies (Order: Diptera), but Lepidoptera are arguably the most important prey taxa and are consumed by virtually all insectivorous bats (Lacki et al. 2007, Dodd 2010). In support of a bottom-up relationship, there tends to be a positive correlation between bat activity and Lepidoptera abundance (Meyer et al. 2004, Morris et al. 2010). However, studies that have evaluated the response of both bats and Lepidoptera to forest management practices have found potential benefits for bats after burning and thinning with negative or neutral responses for Lepidoptera abundance (Schwab 2006, Armitage and Ober 2012, Dodd et al. 2012, Cox et al. 2016). These benefits to bats are not necessarily causing a reduction in Lepidoptera abundance; top-down reductions in overall insect populations have been demonstrated in nighttime enclosure experiments with bats, but reductions in Lepidoptera abundance were not significant (Kalka et al. 2008, Williams-Guillén et al. 2008). Artificially and intentionally constructed clutter decreased the activity of smaller bat species with nocturnal Lepidoptera abundance remaining unchanged (Brigham et al. 1997). This may be the result of open habitats providing more efficient foraging with increased prey encounters and an increase in foraging speed (Norberg 1981). These benefits to bats foraging in open areas may outweigh the potential reductions in prey abundance due to burning and thinning.

Three species of federally endangered bats are known to reside in the Ozark region of Arkansas, including the Indiana bat (*Myotis sodalis*), gray bat (*Myotis*

grisescens), and the Ozark big-eared bat (*Corynorhinus townsendii ingens*), along with the threatened northern long-eared bat (*Myotis septentrionalis*) and other vulnerable species (Harvey et al. 1979, Perry et al. 2018). Due to their control of insect pests, bats are estimated to be worth approximately \$22.9 billion a year to the agricultural industry in the United States alone (Boyles et al. 2011). Declines in insect populations as a result of climate change are associated with declines in insectivorous vertebrate species (Lister and Garcia 2018). If bat abundance is positively associated with Lepidoptera abundance, preserving an abundant Lepidoptera community may be crucial for bat conservation in areas that contain vulnerable species, especially as bat populations continue to rapidly decline due to white-nose syndrome in the United States (Blehert et al. 2009).

Hypotheses and Predictions

The objective of this research was to determine how forest management practices impact insect communities and to determine optimal management and conservation recommendations for preserving woodland pollinators, prey for insectivorous wildlife, and overall insect biodiversity. I hypothesized that a combination of mechanical thinning and intermediate burn frequencies were the best management strategy for promoting insect biodiversity and viability by maintaining woodland habitat. I predicted that:

- 1) Mechanical thinning and greater burn frequencies (4 times in the last 12 years) would be associated with lower tree density and basal area, less canopy cover, and greater proportion of grasses and forbs in the groundcover;
- 2) Lepidoptera diversity would be greatest in stands with intermediate burn frequencies (1–3 times in the last 12 years) that were not thinned;

- 3) Lepidoptera abundance and biomass would be the least in thinned stands with greater burn frequencies (4 times in the last 12 years), and
- 4) The abundance and biomass of Coleoptera would be greatest at intermediate burn frequencies (1–3 times in the last 12 years) with mechanical thinning.

Methods

Site Description

My study was located in the Big Piney Ranger District of the Ozark National Forest in the Lower Boston Mountains of Arkansas (Figure 1). The area I chose for my sites is part of a U.S. Forest Service pine woodland restoration project that involves prescribed burning and mechanical thinning as forest management strategies. The tree composition mostly consisted of shortleaf pine (*Pinus echinata*) and oak (*Quercus*) species, and included red maple (*Acer rubrum*), eastern redcedar (*Juniperus virginiana*), black gum (*Nyssa sylvatica*), black walnut (*Juglans nigra*), and hickories (*Carya* spp.) (De Jong and Zollner 2017).

I received thinning, prescribed burning, and other forest management history data from the U.S. Forest Service. I selected 30 stands: 12 burned and thinned, 12 burned only, and 6 controls (Table 1). I selected 12 burn sites based on the frequency and last year of prescribed burning. All burns were done during the dormant season (January–April), and all sites were burned once in the 2 years prior to sampling (2017 or 2018). This resulted in 6 of the 12 sites being last burned in 2017 and the other 6 being last burned in 2018. I categorized sites based on their burn frequency, which included sites that were burned: A) 1–3 times in the last 12 years (intermediate burn frequency); and B) 4 times in the last 12 years (high burn frequency). Two stands (10–40 ha in size) that

were similar in slope and altitude were selected in each of the 12 sites (Figure 2). These stands represented A) a stand that was only burned; and B) a stand that was burned and thinned. In addition, 6 untreated stands were also selected as controls based on their proximity to treatment sites and similarity in aspect.

Insect Sampling

I deployed Universal Black Light Traps (Bioquip, Rancho Dominguez, CA, USA) with an ultraviolet blacklight and powered by a 12V battery to collect nocturnal Lepidoptera and Coleoptera species to assess presence of insectivorous bat prey. Light traps that use both visible and ultraviolet light, such as the Bioquip blacklight trap, have been shown to be the most effective at attracting Lepidoptera when compared to other types of light traps (Belton and Kempster 1963). I wired the light traps to a 12V programmable timer (Misol, Jiaying City, ZJ, China) so that the light turned on at sunset to maximize sampling time through the night. I hung the light traps from a 1.5 m high Shepherd's hook to control for differences in flight elevation between Lepidoptera families (Taylor and Brown 1972, Lewis et al. 1993). I killed collected specimens in light traps by placing sponges soaked in ethyl acetate in a glass jar sealed with cheese cloth to allow fumes to fill the bucket of the trap (Blanco and Garrie 2020). Despite the 12V batteries only lasting approximately 10 hours, the dead insects sat in the bucket until I collected them 20–28 hours after being deployed (Capaverde et al. 2018).

I conducted sampling over 6 nights every lunar cycle (month), with each stand sampled for 1 night every lunar cycle from late March to early November of 2019. I sampled all stands approximately each lunar cycle to take into account seasonal differences in insect abundance (Selman and Barton 1972). Therefore, I sampled each

stand 8 times over the course of the 9-month period, resulting in 48 sampling nights total. During each sampling night, I collected insects in 1 control stand, 2 stands that were burned and thinned, and 2 stands that were burned only, all of which were grouped in close proximity to each other to maximize sampling efficiency. This resulted 5 stands being sampled during each sampling night. I randomly generated coordinates for sampling points within each stand for each monthly collection night in ArcMap (ESRI, Redlands, CA, USA). When generating the points, I specified in ArcMap that the random points must be >60 m away from each other, as this is the maximum range blacklight traps can attract most Lepidoptera species (Beck and Linsenmair 2006, Truxa and Fielder et al. 2012, Grunsven et al. 2014), and ensured all points were within 50–500 m of a main road. In cases where the stands were too small to fit 8 sampling points within the constraints, stands were combined with an adjacent stand with the same burning and thinning treatments and considered 1 stand. I also placed all light traps during each sampling night in different stands >200 m away from each other to avoid pseudoreplication, as this distance is approximately the maximum dispersal distance of nocturnal Lepidoptera when marked and recaptured (Margaritopoulos 2012).

I avoided sampling nights with heavy rainfall to prevent insect specimens from becoming waterlogged and difficult to identify and to prevent electrical damage to light trap adapters. Rainfall has also been associated with a decrease in Lepidoptera abundance in light traps, biasing the results (Douthwaite 1978, Tucker 1983). I also avoided sample nights within 3–4 days of a full moon (>80% illumination) when possible due to lunar light being associated with a lower Lepidoptera abundance in light traps (Persson 1976, Douthwaite 1978, Taylor 1986, Dent and Pawar 1988, Yela and Holyoak 1997).

However, I frequently broke this rule during the sixth, seventh, and eighth sampling cycles due to scheduling conflicts.

After I retrieved the light traps, the insects were collected and brought back to the lab for storage and sorting. Starting the day of trap retrieval, I placed the specimens in a freezer to ensure death, and then I placed them in a paper bag for drying (Cho et al. 2016). I placed the paper bags in a drying oven at approximately 40° C. I frequently measured the mass of the bags until the mass was stable and no longer decreased to determine when drying process was complete. Finally, I took biomass metrics after fully dried by measuring the mass of the entire sample and specific taxa to the nearest 0.01 g.

Nocturnal, aerial insects, most of which were Lepidoptera and Coleoptera, were collected to assess the presence of bat prey. I identified insects other than nocturnal Lepidoptera to order according to Borror and White (1970) and Gullan and Cranston (2014). For Lepidoptera, I identified all specimens within the clade of Macroheterocera to at least family according to Spencer (2014) and Leckie and Beadle (2018) to have data available for Simpson family diversity index calculations. Macroheterocera includes the larger moths and most of the families traditionally classified as Macrolepidoptera, including Apatelodidae, Drepanidae, Erebiidae, Geometridae, Lasiocampidae, Mimallonidae, Noctuidae, Notodontidae, Saturniidae, and Sphingidae (Mitter et al. 2017). I identified specimens in the families Erebiidae, Notodontidae, and Saturniidae to species for Simpson species diversity index calculations.

I lumped specimens of families not in Macroheterocera together and categorized them as Microlepidoptera. The scope of the project was focused on larger Macroheterocera due to better preservation for identification and because bats tend to

feed on larger Lepidoptera species (Dodd 2006). I assumed unknown Lepidoptera with a total forewing length of ≤ 10 mm were not Macroheterocera, and I categorized them as unknown Microlepidoptera. I assumed unknown Lepidoptera with a total forewing length > 10 mm were unidentified Macroheterocera. I counted Macroheterocera specimens for abundance metrics, but I did not count Microlepidoptera due to the large volume in some traps and because they would often get mixed with large amounts of dead insect debris, making them difficult and time consuming to sort.

I calculated a Macroheterocera family diversity index using Simpson's D. To estimate Lepidoptera species diversity, I calculated both Erebidæ and Notodontidæ species diversity indices using Simpson's D because species richness of these 2 families have been found to be correlated with overall Lepidoptera species richness (Summerville et al. 2004). I also calculated Saturniidæ species diversity due to this family having the highest percentage of individuals that were successfully identified to species. While it was not feasible to calculate overall Lepidoptera species diversity due to the condition of individual specimens collected and the time required for identification, I used these 4 diversity metrics as proxies to observe differences in Lepidoptera diversity between treatments. I did not include unidentified specimens in diversity index calculations.

Environmental Measurements

I took other measurements at each sampling point to account for potential confounding variables. I measured the slope at each sampling point using a clinometer, and I determined the aspect at each sampling point using a compass (Womack 2017). Due to aspect values being circular, I categorized them into 1 of 8 cardinal direction categories. I retrieved the nightly low temperatures ($^{\circ}$ C) from the nearest Remote

Automated Weather Station (RAWS) to each sampling point (Western Regional Climate Center 2019). I also determined the percent moon illumination for each sampling night according to the United States Naval Observatory (2017).

Vegetation Surveys

I measured vegetation characteristics to determine how burn frequency and mechanical thinning influence insect habitat. I measured the diameter at breast height (DBH, cm) of all trees ≥ 10 cm DBH within a circular 11.3-m radius plot around each sampling point and used the measurements to calculate the basal area (m^2/ha) of canopy trees (Zebehazy 2002, Ober 2006, Dodd 2010, Womack 2017). I also counted all canopy trees in the plot to estimate tree density and identified them to genus. I assessed the ground vegetation at each sampling point using a 50×50 cm modified Daubenmire frame, with the percent groundcover of grasses and forbs visually estimated both at the sampling point and 4 m in each cardinal direction, and with the 5 values being averaged for the plot (Daubenmire 1959, Annis 2019). I also estimated canopy cover (% covered) at each of these 5 points using a spherical densiometer (Forestry Suppliers, Jackson, MS, USA), and I then calculated the mean of those numbers for the plot.

Data Analysis

To assess the impact of burn frequency and thinning on insect biomass, abundance, and diversity, I used multi-model selection and AICc values (Akaike Information Criterion adjusted for small sample sizes) to rank candidate insect and vegetation models (Burnham and Anderson 2004). I created 20 linear mixed effects models for each of the 14 continuous insect response variables, including the null model (Table 2). I also created the same models (excluding the models with moon illumination

and temperature) for 5 continuous vegetation response variables to see if burning and thinning had the expected environmental impact (Table 3). Moon illumination and nightly low temperature were excluded from the vegetation models because these variables were included to control for changes in insect activity during the night of sampling.

For all 19 response variables, the null model included lunar cycle (month) as a fixed effect and stand as a random effect to take into account the pseudoreplication associated with resampling the same stands every sampling month. The rest of the models also included different combinations of burn frequency (factor), thinning (factor), the interaction of burn frequency and thinning, nightly low temperature (continuous), and percent moon illumination (continuous) as additional fixed effects (Table 2). With the 20 models for each of the response variables, the preferred model was chosen for each individual response based on having the lowest AICc value. Models with a $\Delta\text{AICc} \leq 2.00$ were considered competitive models (Burnham and Anderson 2004). If the null model did not have the lowest AICc value, whatever fixed effects were in the top model were determined to be the best predictors for the response variable. Due to the estimate (β) and standard error (SE) values changing for a given fixed effect depending on what other covariates are in the model, the reported β and SE values for fixed effects are from the highest ranking model that included that particular fixed effect as a parameter.

Results

Total Insects and Coleoptera

Over the course of the study, I collected 1.55 kg of dry insect biomass from 12 different orders (Table 4). There were a total of 233 successful insect trap collections.

With blacklight traps deployed in 30 stands every sampling month over an 8-month sampling season, I had a total of 5 traps malfunction due to battery and timer issues. This included 1 deployment in a thinned stand that was in the high burn category, 1 in an unthinned stand in the intermediate burn category, 2 in a thinned stand in the intermediate burn category, and 1 in an untreated control stand. I also had 2 sampling efforts disrupted due to U.S. Forest Service management activity in my sites, including another thinned stand in the intermediate burn category and another untreated control stand.

The absence of thinning ($\beta = -0.929 \pm 0.612$ SE), increased temperature ($\beta = 0.257 \pm 0.089$ SE), and decreased moon illumination ($\beta = -0.038 \pm 0.014$ SE) were all associated with a greater total insect biomass (Figures 3 and 4; Table 5). Increased moon illumination was associated with decreased Coleoptera biomass ($\beta = -0.019 \pm 0.004$ SE) and abundance ($\beta = -0.504 \pm 0.108$ SE; Figure 5). Burn frequency resulted in increased Coleoptera abundance at intermediate burn frequencies ($\beta = 0.688 \pm 8.285$ SE) and high burn frequencies ($\beta = 21.389 \pm 8.254$ SE). Competitive models showed an increase in Coleoptera biomass with higher temperatures ($\Delta AICc = 1.28$; $\beta = 0.032 \pm 0.033$ SE) and the presence of thinning ($\Delta AICc = 1.38$; $\beta = 0.210 \pm 0.228$ SE; Table 6).

Lepidoptera

Of the Lepidoptera that I identified as Macroheterocera, I was able to identify 75% to at least family. The most common family was Noctuidae, with 4,617 individuals, followed closely by Geometridae, with 4,118 individuals (Table 7). Of the three families that I tried to identify further than family, 89% of Erebidae were identified to species, 60% of Notodontidae were identified to species, and nearly 100% (all but 1 individual) of Saturniidae were identified to species. This included 79 distinct species of Erebidae, 16

distinct species of Notodontidae, and 7 distinct species of Saturniidae (Table 8). The most common Erebidæ species were the lead-colored lichen moth (*Cisthene plumbea*), the painted lichen moth (*Hypoprepia fucosa*), and the banded tussock moth (*Halysidota tessellaris*). The most common Notodontidae species were the spotted datana (*Datana perspicua*) and the rough prominent (*Nadata gibbosa*), and the most common Saturniidae species was the rosy maple moth (*Dryocampa rubicunda*).

Lepidoptera biomass was lower in thinned stands ($\beta = -1.036 \pm 0.546$ SE) and increased with increasing temperature ($\beta = 0.266 \pm 0.067$ SE). Macroheterocera abundance had the same relationship with thinning ($\beta = -22.139 \pm 11.561$ SE) and temperature ($\beta = 5.620 \pm 1.238$ SE) as Lepidoptera biomass (Figure 6). Competitive models also showed a decrease in Lepidoptera biomass ($\Delta AICc = 0.09$; $\beta = -0.017 \pm 0.011$ SE) and Macroheterocera abundance ($\Delta AICc = 0.26$; $\beta = -0.298 \pm 0.209$ SE) with increasing moon illumination (Table 9).

Geometridæ abundance was also lower in thinned stands ($\beta = -6.399 \pm 3.593$ SE) and increased with increasing temperature ($\beta = 1.046 \pm 0.419$ SE). Geometridæ abundance increased with increasing moon illumination in a competitive model ($\Delta AICc = 2.00$; $\beta = 0.035 \pm 0.071$ SE). Noctuidæ abundance also increased with increasing temperature ($\beta = 1.471 \pm 0.378$ SE) in the top model and decreased with increasing moon illumination ($\Delta AICc = 1.00$; $\beta = -0.071 \pm 0.064$ SE) in a competing model. In another competitive model ($\Delta AICc = 1.35$), Noctuidæ abundance was greater in stands with intermediate burn frequencies ($\beta = 1.706 \pm 4.365$ SE) but lower in stands with high burn frequencies ($\beta = -4.584 \pm 4.346$ SE) compared to the unburned stands (Table 10). Saturniidae abundance was lower in stands with intermediate burn frequencies ($\beta =$

-3.724 ± 3.954 SE) and stands with high burn frequencies ($\beta = -8.677 \pm 3.939$ SE) compared to unburned stands (Figure 7). Saturniidae abundance also increased with increasing temperature ($\beta = 1.395 \pm 0.426$ SE) and moon illumination ($\beta = 0.147 \pm 0.061$ SE) in the top model. In a competitive model ($\Delta AICc = 1.53$), Saturniidae abundance was also lower in thinned stands ($\beta = -3.604 \pm 2.957$ SE; Table 11).

The top model for both Erebidae abundance and Notodontidae abundance was the null model. However, both Erebidae abundance ($\Delta AICc = 1.57$; $\beta = 0.168 \pm 0.211$ SE) and Notodontidae abundance ($\Delta AICc = 1.70$; $\beta = 0.108 \pm 0.150$ SE) increased with increasing temperatures in competitive models (Table 11). Erebidae abundance ($\Delta AICc = 0.36$; $\beta = -0.041 \pm 0.030$ SE) and Notodontidae abundance ($\Delta AICc = 1.86$; $\beta = -0.013 \pm 0.021$ SE) also both decreased with increasing moon illumination in other competitive models. In another competitive model ($\Delta AICc = 0.39$), Erebidae abundance was lower in thinned stands ($\beta = -2.755 \pm 2.016$ SE).

Macroheterocera family diversity increased with increasing temperature ($\beta = 0.018 \pm 0.003$ SE). Macroheterocera family diversity was lower in stands with intermediate ($\beta = -0.043 \pm 0.028$ SE) and high ($\beta = -0.017 \pm 0.028$ SE) burn frequencies compared to unburned stands in a competitive model ($\Delta AICc = 1.77$), and decreased with increased moon illumination in another competitive model ($\Delta AICc = 1.92$; $\beta = -0.0002 \pm 0.0004$ SE). Notodontidae species diversity increased with increasing moon illumination ($\beta = 0.001 \pm 0.0004$ SE) and was greater in stands with high burn frequencies ($\beta = 0.050 \pm 0.038$ SE) compared to unburned stands. Despite Notodontidae species diversity being lower in stands that were thinned ($\beta = -0.086 \pm 0.038$ SE) and lower in stands with intermediate burn frequencies ($\beta = -0.071 \pm 0.039$ SE) compared to untreated stands, the

interaction suggests that Notodontidae species diversity was greater in stands that combined thinning with intermediate burn frequencies ($\beta = 0.138 \pm 0.055$ SE; Figure 8).

The top model for both Erebidae species diversity and Saturniidae species diversity was the null model. However, both Erebidae ($\Delta AICc = 0.53$; $\beta = 0.005 \pm 0.004$ SE) and Saturniidae ($\Delta AICc = 1.12$; $\beta = 0.002 \pm 0.002$ SE) species diversity increased with increasing temperature in competitive models (Table 12). Erebidae species diversity was greater ($\Delta AICc = 1.49$; $\beta = 0.025 \pm 0.056$ SE) and Saturniidae species diversity was lower ($\Delta AICc = 1.45$; $\beta = -0.016 \pm 0.018$ SE) in thinned stands in other competitive models. In an additional competitive model ($\Delta AICc = 0.95$), Erebidae species diversity was lower in stands with intermediate burn frequencies ($\beta = -0.028 \pm 0.039$ SE) but greater in stands with high burn frequencies ($\beta = 0.031 \pm 0.039$ SE) compared to unburned stands. Saturniidae species diversity also decreased with increasing moon illumination in another competitive model ($\Delta AICc = 1.43$; $\beta = 0.0003 \pm 0.0003$ SE).

Vegetation and Environmental Variables

The mean (\pm SE) moon illumination per sample was 35.59% \pm 2.01%. Of the 233 collections, 25 were during nights with >80% moon illumination. The mean (\pm SE) nightly low temperature for a sample was 12.6° \pm 0.46° C. All of the aspect direction categories were represented in the dataset, with the least represented aspect being east-facing slopes (8.5% of the samples) and the most represented aspect being southeast-facing slopes (16.3% of the samples). The mean (\pm SE) slope per sample was a 13.60% \pm 0.55% incline. For groundcover, the mean (\pm SE) grass percentage for a sample was 8.97% \pm 0.88% and the mean (\pm SE) forb percentage was 16.91% \pm 0.91%. For tree measurements, the mean (\pm SE) canopy cover was 87.08% \pm 0.88%, the mean (\pm SE) basal

area was $29.73 \pm 0.91 \text{ m}^2/\text{ha}$, and the mean ($\pm \text{SE}$) tree density was 18.88 ± 0.85 trees in a 11.3-m radius plot. A total of 4,292 trees were measured, with the 2 genera making up 75% of the composition of the stands being *Pinus* spp. (2,120 trees) and *Quercus* spp. (1,123 trees).

Canopy cover ($\beta = -10.314 \pm 3.232 \text{ SE}$), basal area ($\beta = -7.815 \pm 3.167 \text{ SE}$), and tree density ($\beta = -8.572 \pm 3.232 \text{ SE}$) were all lower in thinned stands. In competitive models ($\Delta \text{AICc} = 1.10$), basal area was also lower in stands with intermediate ($\beta = -5.227 \pm 4.568 \text{ SE}$) and high ($\beta = -5.305 \pm 4.564 \text{ SE}$) burn frequencies compared to unburned stands (Table 13). There was less grass in stands with intermediate burn frequencies ($\beta = -0.069 \pm 3.391 \text{ SE}$), but there was more grass in stands with high burn frequencies ($\beta = 6.767 \pm 3.388 \text{ SE}$). There was also more grass ($\beta = 6.557 \pm 2.560 \text{ SE}$) and forbs ($\beta = 5.254 \pm 1.618 \text{ SE}$) in thinned stands. In a competitive model ($\Delta \text{AICc} = 0.04$), there were also more forbs in stands with intermediate ($\beta = 4.758 \pm 2.208 \text{ SE}$) and high ($\beta = 3.245 \pm 2.202 \text{ SE}$) burn frequencies compared to unburned stands. However, in another competitive model ($\Delta \text{AICc} = 1.01$), the interaction suggests that there were less forbs in stands that combined thinning with intermediate burn frequencies compared to untreated stands ($\beta = -3.789 \pm 3.318 \text{ SE}$).

Discussion

Interestingly, not only did my data not support the intermediate disturbance hypothesis as I predicted, but my findings showed the opposite pattern with regards to burn frequency. Erebid species diversity and Notodontidae species diversity, which have both been shown to be good representatives of overall Lepidoptera species diversity (Summerville et al. 2004), were marginally lower in the intermediate burn frequency

stands in either the top model or competitive models. Macroheterocera family diversity was also lowest in the intermediate burn frequency stands, which is inconsistent with the intermediate disturbance hypothesis (Connell 1978, Sousa 1979). A meta-analysis testing the intermediate disturbance hypothesis found that this “U-shaped” relationship between disturbance and species diversity was the least commonly reported relationship (Mackey and Curie 2001). However, species diversity being lowest with intermediate intensities of disturbance has been demonstrated in an agricultural context with ants (Bestelmeyer and Wiens 1996) and in burned forests with birds (Raphael et al. 1987). Lower habitat heterogeneity with intermediate burn frequencies has also been demonstrated in tallgrass prairie (Collins 1992).

Support for the intermediate disturbance hypothesis has declined over time due to results varying depending on the taxa, ecosystem, or type of disturbance involved (Moi et al. 2020). It could be that the “U-shaped” relationship between disturbance and species diversity is a pattern observed specifically with insect communities or in burned habitats. However, insect communities can follow the intermediate disturbance hypothesis (Szentkirályi and Kozár 1991), and plant diversity has shown no relationship with burn frequency in pine savannas (Beckage and Stout 2000). There were also potential biases that could explain my results. Many of the intermediate burn frequency stands were overgrown with briars (*Smilax* spp.) and blackberries (*Rubus* spp.), which could result in visual obstruction of the blacklight. This may have led to a lower number of Lepidoptera from certain taxa being drawn into the light if it was not visible due to dense vegetation. There are also limitations to the fact that not all Lepidoptera specimens were identified to species, and a true Lepidoptera species diversity index was not calculated. However, my

results not supporting the intermediate disturbance hypothesis is consistent with previous findings (Mackey and Curie 2001, Moi et al. 2020), and the concept has even been outright rejected as a universal ecological rule (Collins 1992, Fox 2013).

Consistent with the intermediate disturbance hypothesis (Connell 1978, Sousa 1979), selectively thinned areas in Malaysia had greater Geometridae species diversity compared to unthinned and clearcut areas (Intachat et al. 1997). However, in my study, Geometridae abundance decreased with thinning, and Notodontidae and Saturniidae species diversity decreased marginally with thinning, likely due to their reliance on deciduous trees as hosts (Miller 1992, Butler and Strazanac 2000, Spencer 2014, Leckie and Beadle 2018). Erebidae species diversity showed the opposite pattern, increasing marginally with thinning in a competitive model. This could be because many of the species in Erebidae are lichen moths, and thinning can be beneficial to the lichen community (Root et al. 2010). This is also consistent with research that suggests that thinning could increase Lepidoptera species richness (Thomas 2002). Thinning lowered the canopy cover, basal area, and tree density as expected. The reduction of canopy cover, basal area, and tree density allows more sunlight for forbs and grasses to grow on the forest floor (McConnell and Smith 1970), and it could explain why thinning also consistently changed many insect metrics in my study.

Lepidoptera

Despite marginally increasing Erebidae species diversity, thinning actually decreased Erebidae abundance in a competitive model. This could be due to thinning increasing the diversity of the ground vegetation or lichen community that would provide a diversity of host plants (Dodson et al. 2007, Root et al. 2010), but decreasing the

deciduous trees that also act as hosts and could contribute to lower Erebidae abundance (Butler and Strazanac 2000, Spencer 2014, Leckie and Beadle 2018). Despite being present in the diet of many bat species (Dodd 2010, Riccucci and Lanza 2014, Aizpurua et al. 2017), tiger moths (Arctiinae spp.), which make up the majority of collected Erebidae, have a myriad of methods to avoid being consumed by bats. Some species, including the commonly caught *Halysidota tellularis* and *Hypoprepia fucosa*, use toxic chemicals consumed from plants to deter bats from eating them, rendering the moths unpalatable (Hristov and Conner 2005). Tiger moths also have the ability to give off clicking sounds that disrupt bat echolocation when they are attempting to forage (Corcoran et al. 2009). These clicking sounds can also deter bats by scaring them off, and the bats also learn to associate the clicking sounds with the unpalatability of the moths, leading them to avoid this taxa when foraging (Bates and Fenton 1990). Despite being a good indicator of Lepidoptera diversity (Summerville et al. 2004), Erebidae do not seem to be an important family to focus on in terms of maximizing abundance as a source of bat prey.

Noctuidae was the most abundant Lepidoptera family in my study and in other studies (Burford et al. 1999, Summerville and Crist 2002, Summerville and Crist 2003, Schwab 2006, Dodd et al. 2008, Dodd et al. 2011). Molecular analyses and fecal identifications of bat guano suggest that the Macroheterocera family that bats primarily feed on is Noctuidae (Dodd 2010, Riccucci and Lanza 2014, Aizpurua et al. 2017). Although Lepidoptera diversity did not follow the prediction from the intermediate disturbance hypothesis (Connell 1978, Sousa 1979), Noctuidae abundance was marginally greater in stands burned at intermediate frequencies in a competitive model.

Noctuidae larvae abundance has been found to be greater in stands burned every 4 years when compared to unburned stands and stands burned at least every 2 years (Hanula and Wade 2003). This could indicate that occasional burning may be good for Noctuidae, but burning at high frequencies could be detrimental to the most important Lepidoptera family for bat forage. However, if the bats are feeding opportunistically (Brack and LaVal 1985), maximizing total nocturnal, aerial insect biomass in general may be more important than maximizing the abundance of specific families.

Geometridae primarily use deciduous trees and forbs as hosts (Niemelä et al. 1982, Butler and Strazanac 2000, Spencer 2014, Leckie and Beadle 2018), and the removal of these hosts to promote pine savanna habitat could reduce the abundance of Geometridae. Total insect biomass, Lepidoptera biomass, Macroheterocera abundance, and Geometridae abundance all being lower in thinned stands is likely 4 observations of the same relationship because the only Macroheterocera family that was negatively associated with thinning was Geometridae, which was the second most abundant Macroheterocera family in my study. This is consistent with findings that stand harvest can lower Lepidoptera abundance (Summerville 2011, Summerville et al. 2013). Potential increases in forbs as a result of thinning may not provide enough Geometridae hosts to counteract the removal of tree hosts. Saturniidae showed decreases in abundance with increasing burn frequency and with thinning. This may be because many Saturniidae only reproduce once a year (Allen 1976), whereas most of the other moth families reproduce multiple times a year in middle latitudes (Pöyry et al. 2011). This life history trait may make it more difficult for populations of this family to rebound after a

disturbance. While burning at high frequencies may not impact Lepidoptera biomass or abundance overall, it may have a negative impact on specific taxa.

The Saturniidae species *Actias luna* emerges sooner from the pupae stage when they are exposed to 16-hour photoperiods compared to 24-hour photoperiods (Wright 1970), indicating that Saturniidae do not emerge faster due to the light of a full moon. However, in my study, Saturniidae abundance was greater when there was more moonlight, and any Saturniidae that has been captured has recently emerged from the pupae stage, since they do not feed as adults and only live for 5–12 days (Janzen 1984). The observed relationship between Saturniidae and moon illumination is the opposite of what was observed for Lepidoptera as a whole and most other Lepidoptera families in competitive models. Lepidoptera are believed to be attracted to light because they use the moon for navigation, and if the moon is visible during a given night, it is a much larger and attractive light source than the trap (Lees and Zilli 2019). However, studies using baited traps without light to control for biases suggest there is no significant relationship between moonlight and nightly Lepidoptera activity (Yela and Holyoak 1997). More research needs to be done to determine if the specific family of Saturniidae changes its flight behavior or pupae emergence rates when there is more moonlight.

All of the Lepidoptera diversity indices except Notodontidae species diversity were greater with increased temperature likely because a greater abundance of Lepidoptera tend to be captured with warmer temperatures (Yela and Holyoak 1997). On colder nights, and nights with high moon illumination, I often caught 0 or 1 Lepidoptera specimens, which leads to very low diversity numbers and hence a negative association with colder temperatures. Macroheterocera family diversity was marginally lower with

higher moon illumination, which could also be due to very low abundances resulting in low diversity index calculations.

Notodontidae species diversity could be lower with thinning because deciduous trees are a major host for Notodontidae species (Miller 1992, Butler and Strazanac 2000, Spencer 2014, Leckie and Beadle 2018). The increase in Notodontidae species diversity with the interaction between intermediate burn frequencies and thinning could be explained by the interaction between burning frequency and thinning increasing the diversity, but not necessarily the abundance, of the ground vegetation (Dodson et al. 2007). However, drawing conclusions from the patterns observed with Notodontidae species diversity should be done with caution because Notodontidae had the fewest successful identifications compared to the other taxonomic groups with calculated diversity indices. In addition, many species of Notodontidae, including the most abundant *Datana perspicua*, are associated with weedy sumac trees (*Rhus* spp.) and can be a pest to native plants in the southeastern United States (Crocker and Simpson 1982, Spencer 2014, Leckie and Beadle 2018). The walnut caterpillar moth (*Datana integerrima*), another common Notodontidae species, is a defoliating pest of black walnut (*Juglans nigra*) trees (Farris and Appleby 1979). Therefore, potential decreases to Notodontidae species diversity due to thinning may not necessarily be a bad thing if it is an indicator of the presence of plant or insect pests.

Coleoptera

Coleoptera biomass and abundance, and total insect biomass, decreased with an increase in moon illumination, which is also consistent with previous insect research in the Arkansas Ozarks (Blanco and Garrie 2020). This could be because the light from the

blacklight trap is brighter and more attractive compared to the lack of natural ambient light of the night (Bowden and Church 1973). Despite other studies finding decreases in Coleoptera abundance with increased burn frequency (Siemann et al. 1987), my results showed Coleoptera abundance increased with burn frequency. The majority of the Coleoptera collected were *Phyllophaga* spp., which have many host plants in Arkansas including a variety of forbs and deciduous trees (Sanderson 1944). Since my results showed that burning increases forbs but does not decrease tree density, burning may be maximizing the abundance of Coleoptera host plants. However, Coleoptera biomass was greater in thinned stands in a competitive model, suggesting that the increase in forb hosts from thinning may be a stronger driver of Coleoptera biomass than the density of tree hosts.

Vegetation

It is surprising that increased burn frequency only decreased basal area in competitive models, since burning trees should also lower the canopy cover and burn away smaller trees, which would also lower the tree density (Scherer et al. 2016). This would theoretically, just like with thinning, promote the growth of grass and forbs as a result (Hutchinson et al. 2005). My results showing that canopy cover and tree density are not lower with increasing burn frequency is likely due to the fact that over half (53%) of the fires were low intensity ground fires and not high intensity crown fires. Low intensity fires are intense enough to burn away litter and fuel on the forest floor, which would allow grasses to grow, but not intense enough to burn canopy trees to the point of removal or death (Brose and Van Lear 1999, Dey and Hartman 2005). Interestingly, grass groundcover was lowest in the intermediate burn category, likely due to many of the

intermediate burn frequency stands being overgrown with briars and blackberries.

Greater burn frequencies keep the amount of shrubs down, allowing there to be less competition for grasses to grow (Hodgkinson and Harrington 1985).

Conclusions

Consistent with the mixed results of past studies (Swengel 2001), the effects of prescribed burning tend to vary depending on taxa. Thinning appears to be detrimental to total nocturnal, aerial insect biomass and Lepidoptera abundance and biomass, but may provide marginal increases in Erebidae species diversity, which can be an indicator of overall Lepidoptera species diversity (Summerville et al. 2004). The intermediate and high burn frequency categories both presented their own advantages and disadvantages to insect abundance and diversity. High burn frequencies may lower the abundance of Saturniidae and Noctuidae, but do not seem to lower Lepidoptera biomass or abundance as a whole. This could be detrimental to bats if they specialize on Noctuidae, and intermediate burn frequencies could be an alternative to preserve bat prey since Noctuidae abundance was also marginally greater in stands with intermediate burn frequencies compared to unburned stands. However, total nocturnal, aerial insect biomass is likely more important to bat conservation due to bats feeding on a myriad of insect orders (Lacki et al. 2007, Dodd 2010, Aizpurua et al. 2017). Intermediate burn frequencies were also associated with lower Erebidae and Notodontidae species diversity and lower Macroheterocera family diversity, which could be indicators of forest health (Wang et al. 2008).

Burning at high frequencies appears to maximize Lepidoptera diversity and Coleoptera biomass and abundance without lowering overall nocturnal, aerial insect

biomass or Lepidoptera biomass and abundance. However, thinning did lower total nocturnal, aerial insect biomass and Lepidoptera biomass and abundance, and it was not associated with as many benefits as burning. I therefore recommend that burning at a high frequency (4 times per 12 years, or once every 3 years) and not thinning is best for maintaining an abundant insectivorous bat prey base. Prescribed fire represents a naturally occurring disturbance that the ecosystem is adapted to, with wildfires covering a large area, and disturbances that remove trees, such as tornadoes, occurring in a much smaller area (Outcalt 2008). However, bat activity is normally higher in thinned stands and more open areas with lower basal area (Humes et al. 1999, Blanco and Garrie 2020). This may be because bats expend less energy when they do not have to avoid clutter while foraging (Kalcounis and Brigham 1995). It is possible that the reduction in nocturnal, aerial insect biomass in thinned stands is due to an increase in bat feeding activity, resulting in top-down control (Kalka et al. 2008, Williams-Guillén et al. 2008). Perhaps creating a heterogeneous landscape with unthinned stands that harbor more insects, and thinned stands that provide feeding habitat for bats is the best way to balance these 2 factors regarding bat foraging. The trophic relationships between plants, insects, and bats are complex, and more research needs to be done to determine whether vegetation hosts or vertebrate predators are a stronger driver of insect biomass and abundance.

CHAPTER 2:

WOODLAND GROUND VEGETATION AS A POTENTIAL DRIVER OF POLLINATOR BIOMASS, ABUNDANCE, AND DIVERSITY

Introduction

Background

Pollinators play an important role in plant reproduction in pine (*Pinus*) forest and oak (*Quercus*) woodland ecosystems and can vary in diversity and abundance depending on different forest management practices (Potts et al. 2006). Not only do the orders Lepidoptera (butterflies and moths), Coleoptera (beetles), Diptera (flies), and Hymenoptera (ants, bees, sawflies, and wasps) comprise the prey base for insectivorous bats (Lacki et al. 2007), these orders are also important pollinators (Memmott 2002). Despite the general findings that burning tends to improve the habitats for insectivorous bats (Perry 2012), the impacts of prescribed fire on insects as a whole is mixed (Swengel 2001). One reason for inconsistent results could be that frequency of burning is not taken into account. If intermediate burn frequencies (1–3 times in 12 years, rather than 4 times in 12 years) support a more diverse insect community, the relationship between insects and burning could be consistent with the intermediate disturbance hypothesis (Connell 1978, Sousa 1979). Lower burn frequencies can maintain the presence of rarer native insect species with lower dispersal abilities (Buddle et al. 2006, Atchison et al. 2018). This could be due to generalist invasive species being adapted to colonize high intensity disturbed areas compared to specialist native species (Belote et al. 2008).

Findings on pollinator response to fire over time range from long-term declines in abundance (Potts et al. 2003) to eventual population recovery (Moretti et al. 2006). A

meta-analysis of 2,820 scientific articles on fire and pollinators concluded that fire tends to benefit pollinators, especially Hymenoptera, with the exception of Lepidoptera, which showed decreases in abundance after fire (Carbone et al. 2019). However, this meta-analysis combined studies over a wide range of ecosystems on every continent except Antarctica, and results varied by specific ecosystem type and geographic location.

Pollinators are estimated to be worth approximately \$176 billion to the global agricultural industry (Gallai et al. 2009). As pollinator populations continue to decline due to anthropogenic land-use, invasive species, and climate change (Potts et al. 2010), efforts must be made to preserve insects that provide ecosystem services in order to ensure global food security in the face of a continually growing human population.

Pollinators, Burning, and Thinning

Although prescribed burning may provide an overall benefit to pollinators, it poses a risk by directly killing both ground nesting and cavity nesting bees (*Anthophila* spp.) (Potts et al. 2003, Cane 2011). This is specifically a concern because *Lasioglossum* (Family: Halictidae) is the most abundant and diverse bee pollinator genus in some southern pine savannas (Bartholomew 2004), and they primarily nest in the ground (Wcislo et al. 1993). Despite this, the diversity and abundance of Hymenoptera pollinators, including bees, increases in the understory, but not the midstory, after burning and a combination of burning and thinning (Campbell et al. 2018). This likely results from changes in understory vegetation, with the abundance of bumble bees (*Bombus* spp.) and flowering plants simultaneously increasing in abundance following a burn (Mola and Williams 2018). Stands with greater burn frequencies have a greater richness of non-native Hymenoptera species, indicating that intermediate burn

frequencies may be best for preventing the spread of exotic invasive species (Atchison et al. 2018). However, more frequent burning has been found to be best for maximizing arthropod diversity in longleaf pine (*Pinus palustris*) ecosystems (Nighohossian 2014).

While not as important as Hymenoptera, both Coleoptera and Diptera can act as woodland pollinators. In an oak woodland, thinning with a 25% harvest was ideal for maintaining some Coleoptera and Diptera species assemblages (Økland et al. 2008).

Hymenoptera, Diptera, and Coleoptera abundance was greatest in oak forest stands that received both mechanical shrub removal and prescribed fire treatments, presumably due to increased bare ground for nesting and increased flowering vegetation for foraging (Campbell et al. 2007). The increase in Diptera abundance could also be due to a preference for open habitats by these species (Jacobs 1999). However, in oak savanna habitat, there was a decrease in the proportion of Diptera individuals in the arthropod community with an increased fire frequency (Siemann et al. 1997).

While there were no direct differences in abundance between burned and unburned sites, Coleoptera abundance was negatively associated with basal area in the Arkansas Ozarks (Blanco and Garrie 2020), and prescribed burning tends to lower stand basal area (Scherer et al. 2016). The biomass of Coleoptera and Hymenoptera did not significantly change over the course of a year since the last prescribed burn in a North Carolina longleaf pine forest (Chitwood et al. 2017). In a Mediterranean pine forest, fire increased the abundance, but not diversity, of Diptera, as well as significantly changed the species composition of bees (Lazarina et al. 2017). In Florida pine flatwoods there was a decrease in abundance and family richness of Diptera and Hymenoptera following

dormant season burns (Willcox and Giuliano 2015), whereas these same taxa increased in abundance after a burn in a Kansas prairie (Nagel 1973).

Pollinators and Vegetation

Burning and other disturbances can directly affect insect populations by lowering the numbers of specific taxa immediately (Dunwiddie 1991). However, in a Louisiana pine savanna, burning resulted in an increase in bee abundance and species richness as soon as 2 months post-burn (Bartholomew 2004). The bulk of the long-term changes to the pollinator community due to fire and thinning are likely due to changes in the vegetation, with native plant species richness predicting nearly half of the insect species richness in prairie reserves (Panzer and Schwartz 1998). These vegetation changes affect food resources, habitat, the visibility of flowers that attract pollinators, and trees that act as hosts for Lepidoptera or are used as nests for Hymenoptera (García et al. 2016, Barton and Menges 2018). Pollinators may benefit from the early successional habitat induced shortly after a disturbance (Taki et al. 2013, Bogusch et al. 2015), but the abundance and diversity of these individuals may decline over time as the plant community transitions into later successional stages (Odanaka and Rehan 2020). This change in the insect population coincides with the plant community becoming less diverse via competitive exclusion and overgrown woody species blocking sunlight for forbs and grasses (Peterson and Reich et al. 2008). However, if burns occur too frequently, there may not be enough time for certain flowering plants to reach maturity and hence the plants are burned before they can provide food for certain insect taxa (Pausas and Keeley 2014). There may be a “sweet spot” in terms of disturbance frequency in which the vegetation is

most ideal for pollinators and the number of pollinator species able to coexist is maximized.

The ideal vegetation community for pollinator abundance and diversity could be made up of many factors. In the understory, an abundance of flowering forbs would be the most obvious necessity as they act as a food source for many Hymenoptera and Lepidoptera species (Dumroese et al. 2016). However, grass can also be a host for Lepidoptera species (Wiklund 1984, Spencer 2014). Many wasps and bees rely on bare ground (Potts et al. 2005), dead plant detritus such as leaves and pine needles (Grundel et al. 2010), and large woody debris such as dead logs for nest building (Harmon et al. 1986). Burning and thinning could increase the presence of some habitats and decrease others, making it difficult to predict if there will be a net increase or decrease in abundance and diversity of pollinators. For example, thinning may remove tree hosts but increase ground vegetation hosts, and burning may decrease ground litter, but increase large, dead woody debris. Striking a balance in which there is a diversity of plant and groundcover types and no single microhabitat dominates the community may be important for maintaining an abundant and diverse pollinator community.

Hypotheses and Predictions

The objective of my study was to determine what vegetation variables are most important for preserving woodland pollinators in land managed with prescribed fire and mechanical thinning. Overall, I hypothesized that pollinators would be more abundant and diverse when there was more vegetation, including both trees and ground vegetation. Therefore, I predicted that:

- 1) Total insect biomass and insect family diversity would be negatively associated with canopy cover
- 2) Lepidoptera abundance and biomass would be positively associated with tree density and woody vegetation
- 3) Lepidoptera species diversity would be negatively associated with canopy cover and positively associated with forbs or grass
- 4) Hymenoptera abundance, biomass, and diversity would all be negatively associated with canopy cover and positively associated with forbs
- 5) Coleoptera would be negatively associated with basal area
- 6) Diptera biomass and abundance would be positively associated with canopy cover

Methods

Site Description

My study was in the Big Piney Ranger District of the Ozark National Forest in Pope, Conway, Van Buren, and Johnson counties (Figure 1). Sites consisted mostly of second-growth forest, woodlands, and savannas. Common groundcover species included rosette grass (*Dichanthelium* spp.), little bluestem (*Schizachyrium scoparium*), poverty oat grass (*Danthonia spicata*), rushfoil (*Croton* spp.), woodland sunflower (*Helianthus divaricatus*), Canadian black snakeroot (*Sanicula canadensis*), poison ivy (*Toxicodendron radicans*), muscadine (*Vitis rotundifolia*), cat greenbrier (*Smilax glauca*), and raspberries, blackberries, and dewberries (*Rubus* spp.) (De Jong and Zollner 2017).

I received forest management history data from the U.S. Forest Service.

Vegetation assemblages within sites varied greatly because of the wide range of forest

management strategies. I selected 30 stands (10–40 ha in size) that varied in burn frequency and thinning status in the last 12 years. All burned stands received dormant season (January–April) burns and were burned once in the last 2 years (2017–2018). Six stands were selected in each of 5 treatment categories, all with different combinations of burn frequency and thinning status (Table 1). This included 6 untreated stands that had not been burned or thinned in the last 12 years.

Insect Sampling

During each sampling day, I deployed a white malaise trap (Bioquip, Rancho Dominguez, CA, USA) in each stand being sampled. Malaise traps have been found to be the most effective trapping method for Hymenoptera, the most important order of pollinators, when compared to yellow pan traps and flight intercept trapping (Noyes 1989). I set malaise traps on the same day in different stands >300 m away from each other for independence, as this is the maximum distance bees tend to travel from the nest to feed (Lindauer 1956). I killed insects by placing a cotton ball soaked in ethyl acetate in a small glass test tube in the collection container of each malaise trap. I collected the malaise traps 20–28 hours after being deployed. When I retrieved the traps, insects were brought back to the lab for storage and sorting. Starting the day of trap retrieval, I placed the specimens in a freezer to ensure death and then placed them in a paper bag for drying (Cho et al. 2016). Samples were dried in the paper bags in a drying oven at approximately 40° C. I frequently measured the mass of the bags until the mass was stable to determine when drying process was complete.

Due to differences in insect abundance, biomass, and species composition between months (Selman and Barton 1972), I collected insects at all stands each lunar

cycle (month). I sampled insects for 6 days every lunar cycle from late March through early November of 2019, resulting in stands being sampled 8 times over the course of a 9-month period. This resulted in 48 sampling days. I randomly generated the coordinates for sampling points within each stand for each monthly collection day in ArcMap (ESRI, Redlands, CA, USA). I specified in ArcMap that the random points must be >60 m apart and within 50–500 m of a main road (Figure 2). If a stand was too small to fit 8 sampling points, the stand was combined with an adjacent stand with the same burning and thinning treatment. Typically, I collected insects at random points in an untreated stand and 4 stands with varying burn frequencies and thinning statuses. I avoided days with heavy precipitation when possible to avoid sampling biases associated with rainfall.

I determined biomass after samples were fully dried by measuring the mass of the sample and specific taxa to the nearest 0.01 g. I counted and measured the mass of all Diptera but did not identify them due to Diptera not being the focus of the study and the time and skill required to identify the large volume of Nematocera specimens collected. I counted, measured the mass, and identified Hymenoptera to the lowest taxon possible within a reasonable time (species, genus, or family) according to Eaton and Kaufman (2007) and Wilson and Carril (2015). For Lepidoptera, I also counted, measured the mass, and identified specimens to the lowest taxon possible according to Spencer (2014) and Leckie and Beadle (2018). I counted and identified all insects other than Diptera, Hymenoptera, and Lepidoptera to the lowest taxon possible according to Borror and White (1970) and Gullan and Cranston (2014). Specimens identified to be within taxa of pollination importance were noted. I calculated diversity indices using Simpson's D based on the taxonomic level that had the most consistency in identifications. I calculated

a genus diversity index for Hymenoptera, a species diversity index for Lepidoptera, and an overall insect family diversity index. However, this latter family diversity index excluded Diptera due to lack of identification.

Vegetation and Environmental Variables

At each sampling point, I measured the slope using a clinometer and determined the aspect using a compass (Womack 2017). I then categorized the aspect value into 1 of the 8 categories based on the direction: north, northwest, northeast, west, east, south, southwest, or southeast. I determined tree composition in a circular 11.3-m radius plot around each sampling point; the genus was identified and the diameter at breast height (DBH, cm) was measured for each tree ≥ 10 cm DBH in order to calculate the basal area (m^2/ha) of canopy trees (Zebehazy 2002, Ober 2006, Dodd 2010, Womack 2017). I estimated canopy cover (% covered) at the sampling point and 4 m away in each cardinal direction using a spherical densiometer (Forestry Suppliers, Jackson, MS, USA), averaging the 5 values. Ground vegetation cover was assessed at a different random point elsewhere in the same stand using a 50×50 cm modified Daubenmire frame. This was done at a different point to get a random sample of the ground vegetation of the stand itself and not the microhabitat of the specific malaise trap point being sampled that day. I visually estimated the percent groundcover of grasses, forbs, woody vegetation (shrubs and saplings), litter, and bare ground at this point and 4 m in each cardinal direction, with the 5 values being averaged for the estimate (Daubenmire 1959, Annis 2019).

Data Analysis

Using multi-model selection and AICc values (Akaike Information Criterion adjusted for small sample sizes) (Burnham and Anderson 2004), I assessed the

relationship between vegetation in the managed stands and the insect biomass, abundance, and diversity by creating 24 candidate linear mixed effects models for each of the 12 insect response variables, including the null model (Table 14). For the response variables, the null model included lunar cycle (month) as a fixed effect and stand as a random effect to take into account the pseudoreplication associated with resampling the same stands every month. Most of the models included 2 additional fixed effects: 1 tree variable of 3 possible tree variables and 1 groundcover variable of 5 possible groundcover variables (Table 14). Every combination of tree variable paired with a groundcover variable was represented in the models. Individual models did not include multiple tree variables or multiple groundcover variables due to the inherent collinearity between tree metric variables and between groundcover percentage variables. Univariate models with each individual tree and groundcover variable were also created and included in the model selection process.

With the 24 candidate models for each of the response variables, I chose the model with the lowest AICc value as the preferred model. Any model with a $\Delta\text{AICc} \leq 2.00$ was considered a competitive model (Burnham and Anderson 2004). If the null model was not the top model, fixed effects in the top models were determined to be the best predictors for the response variable. If the standard error (SE) for one of the fixed effects was greater than the estimate (β) in the top model, then the next top model that did not have a covariate with this issue was also considered a competitive model if the model had a $\Delta\text{AICc} \leq 4.00$. Due to β and SE values changing for a given fixed effect depending on what other covariates are in the model, the reported β and SE values for fixed effects are from the highest ranking model that included that particular fixed effect as a

parameter. The means per sampling point of the 8 vegetation variables within each of the 5 burn frequency and thinning treatment combinations were compared using 95% confidence intervals (CI) to put the vegetation relationships in the top insect models in the context of forest management recommendations.

Results

Total Insects

I collected 195.68 g of dry insect biomass. Mean (\pm SE) biomass in a typical trap was 0.82 ± 0.09 g, and the trap with the most biomass was 11.96 g. Most of the biomass was Diptera, making up 75% of the total biomass, followed by Lepidoptera (12%), Hymenoptera (4%), and Coleoptera (2%), with the remaining 7% comprising 8 other insect orders (Table 15). There were a total of 238 successful insect trap collections. Malaise traps were deployed in 30 stands every sampling month over an 8-month sampling season, and sampling efforts were disrupted during 1 sampling day due to U.S. Forest Service management activity in 1 thinned stand in the intermediate burn category and 1 untreated control stand.

Less litter ($\beta = -0.002 \pm 0.0008$ SE) and canopy cover ($\beta = -0.002 \pm 0.001$ SE) were associated with greater insect family diversity (Table 16). More woody vegetation ($\Delta\text{AICc} = 0.70$; $\beta = 0.003 \pm 0.002$ SE) and less basal area ($\Delta\text{AICc} = 1.17$; $\beta = -0.003 \pm 0.001$ SE) were also associated with greater insect family diversity in competitive models (Table 17). Lower tree density resulted in greater total insect biomass ($\beta = -0.008 \pm 0.006$ SE). Competitive models also suggested that lower basal area resulted in greater total insect biomass ($\Delta\text{AICc} = 1.41$; $\beta = -0.001 \pm 0.005$ SE), and more bare ground

($\Delta\text{AICc} = 1.17$; $\beta = 0.013 \pm 0.013$ SE) and woody vegetation ($\Delta\text{AICc} = 0.36$; $\beta = 0.009 \pm 0.006$ SE) also resulted in more total insect biomass (Table 17).

Diptera

Lower tree density resulted in greater Diptera biomass ($\beta = -0.006 \pm 0.006$ SE) and Diptera abundance ($\beta = -0.377 \pm 0.163$ SE; Table 18). More woody vegetation was associated with greater Diptera biomass ($\Delta\text{AICc} = 0.04$; $\beta = 0.009 \pm 0.006$ SE) and abundance ($\Delta\text{AICc} = 1.53$; $\beta = 0.149 \pm 0.184$ SE) in competitive models. In other competitive models, there was lower Diptera biomass with increasing basal area ($\Delta\text{AICc} = 0.66$; $\beta = -0.0006 \pm 0.005$ SE), forbs ($\Delta\text{AICc} = 1.74$; $\beta = -0.005 \pm 0.005$ SE), and grass ($\Delta\text{AICc} = 1.92$; $\beta = -0.003 \pm 0.005$ SE).

Coleoptera

I collected 282 Coleoptera, of which the most common families were 38% Coccinellidae (lady beetles), 6% Curculionidae (true weevils), and 3% Cantharidae (soldier beetles). Less basal area ($\beta = -0.039 \pm 0.027$ SE) and more bare ground ($\beta = 0.223 \pm 0.068$ SE) resulted in a greater Coleoptera abundance, and less canopy cover ($\beta = -0.0008 \pm 0.0003$ SE) and more bare ground ($\beta = 0.002 \pm 0.0009$ SE) resulted in more Coleoptera biomass (Table 18). Lower tree densities were also associated with a greater Coleoptera abundance in a competitive model ($\Delta\text{AICc} = 1.88$; $\beta = -0.00004 \pm 0.0009$ SE).

Hymenoptera

I collected 747 individual Hymenoptera (Table 19). Of the most common families, 37% were Halictidae (sweat bees), 13% were Sphecidae (thread-waisted wasps), and 13% were Ichneumonidae (Ichneumon wasps). I successfully identified 78% of

Hymenoptera to genus, but I was only able to identify 21% to species. The most common Hymenoptera I identified to species was *Dasymutilla quadrigutta*, a velvet ant. The most common Hymenoptera I identified to genus was the sweat bee *Augochlorella*.

Decreased canopy cover ($\beta = -0.002 \pm 0.0003$ SE) and increased grass ($\beta = 0.0008 \pm 0.0004$ SE) resulted in a greater Hymenoptera biomass (Figures 9 and 10), and decreased canopy cover ($\beta = -0.112 \pm 0.022$ SE) and litter ($\beta = -0.028 \pm 0.013$ SE) were associated with a greater Hymenoptera abundance (Figures 11 and 12). There was also an increased Hymenoptera abundance with increased woody vegetation in a competitive model ($\Delta AICc = 1.88$; $\beta = 0.042 \pm 0.027$ SE). Decreased canopy cover ($\beta = -0.005 \pm 0.001$ SE) and increased woody vegetation ($\beta = 0.003 \pm 0.002$ SE) were associated with a greater Hymenoptera genus diversity (Table 20; Figures 13 and 14). There was also a lower Hymenoptera genus diversity with increased litter in a competitive model ($\Delta AICc = 0.63$; $\beta = -0.028 \pm 0.014$ SE).

Lepidoptera

I collected a total of 937 individual Lepidoptera (Table 21), of which the most common families were 15% Nymphalidae (brush-footed butterflies), 15% Hesperiidae (skippers), 4% Lycaenidae (gossamer-winged butterflies), and 3% Papilionidae (swallowtail butterflies). Despite making up the most abundant Lepidoptera families, butterflies were only 38% of the Lepidoptera collected, with the majority being moths. The Lepidoptera species I most frequently caught were *Vanessa atalanta* (red admiral) and *Thorybes pylades* (northern cloudywing).

The top model for Lepidoptera biomass included tree density and bare ground ($\beta = 0.006 \pm 0.002$ SE) as the model parameters. However, the standard error for tree density

was greater than the absolute value of the estimate ($\beta = -0.0005 \pm 0.0009$ SE). The same issue was present with the second ranked model with basal area and bare ground as the model parameters ($\Delta\text{AICc} = 0.33$), with basal area having a standard error greater than the estimate ($\beta = -0.00007 \pm 0.0008$ SE). Therefore, the model with the third lowest ΔAICc value was also considered competitive ($\Delta\text{AICc} = 3.98$). Based on this model, less canopy cover ($\beta = -0.002 \pm 0.0007$ SE) and more bare ground ($\beta = 0.006 \pm 0.002$ SE) resulted in greater Lepidoptera biomass.

A greater abundance of Lepidoptera was associated with a greater tree density ($\beta = 0.021 \pm 0.032$ SE; Figure 15) and less litter ($\beta = -0.052 \pm 0.017$ SE; Figure 16). In a competitive model ($\Delta\text{AICc} = 0.32$), there was also an increase in Lepidoptera abundance with increased basal area ($\beta = 0.009 \pm 0.029$ SE; Table 22). There was an increased Lepidoptera species diversity with a decrease in basal area ($\beta = -0.003 \pm 0.001$ SE) and litter ($\beta = -0.002 \pm 0.0008$ SE). There was also an increased Lepidoptera species diversity with increased grass ($\Delta\text{AICc} = 0.27$; $\beta = 0.004 \pm 0.001$ SE; Figure 17) and decreased tree density ($\Delta\text{AICc} = 0.67$; $\beta = -0.003 \pm 0.001$ SE) in competitive models (Figure 18).

Vegetation and Environmental Variables

The mean (\pm SE) temperature for the samples was $23.44 \pm 0.46^\circ\text{C}$, with daily high temperatures ranging from 4.4°C to 32.8°C . All aspect direction categories were represented in the dataset, with the least represented aspect being east-facing slopes (8.4% of the samples) and the most represented aspect being southeast-facing slopes (15.9% of the samples). The mean (\pm SE) slope per sampling point was a $13.60\% \pm 0.55\%$ incline. The mean (\pm SE) groundcover percentages for a sample were $58.29\% \pm 1.61\%$ litter, $17.15\% \pm 0.91\%$ forbs, $10.45\% \pm 0.75\%$ woody vegetation, $8.92\% \pm 0.87\%$ grass,

and $3.75\% \pm 0.35\%$ bare ground. There was more grass and less litter in plots burned at high frequencies, and there was more grass and woody vegetation in plots within thinned stands (Figure 19). For tree measurements, mean (\pm SE) canopy cover was $87.01\% \pm 0.93\%$, mean (\pm SE) basal area was $29.12 \pm 0.90 \text{ m}^2/\text{ha}$, and the mean (\pm SE) tree density was 18.59 ± 0.84 trees in an 11.3-m radius plot. Canopy cover, basal area, tree density, and litter were all lower in plots within thinned stands (Figure 20). A total of 4,292 trees were measured, with *Pinus* spp. (2,120 trees) and *Quercus* spp. (1,123 trees) making up 75% of stand composition.

Discussion

Consistent with my hypotheses, total insect biomass, Hymenoptera abundance, and Lepidoptera biomass were all maximized when both the canopy cover and litter were low, indicating that maximizing groundcover vegetation is beneficial to pollinators. However, despite being an important food source for Hymenoptera and Lepidoptera (Dumroese et al. 2016), flowering forbs did not seem to be the most important groundcover vegetation for pollinators. In fact, Diptera biomass was lower when there were more forbs in competitive models. Both grass and woody vegetation seem to be more important for pollinator abundance, biomass, and diversity. Despite other findings that suggest that plant species richness decreases with increasing woody vegetation (Peterson and Reich 2008), Hymenoptera abundance and genus diversity, Diptera biomass and abundance, and total insect family diversity were all greater when there was more woody vegetation in either the top model or a competing model. Lepidoptera species diversity and Hymenoptera biomass were both greater when there was more grass in the top model or competitive models, likely due to these taxa utilizing grass for habitat

or as a food source (Wiklund 1984, Dawah and Rothfritz 1995, Immelman and Eardley 2008, Spencer 2014).

Important Species

Many of the bees I collected are important pollinators of woodland flowering plants. This includes Halictidae, the most abundant Hymenoptera family collected, and Apidae, another relatively abundant family in my study. Despite being an important genus in southeastern United States pine savannas (Bartholomew 2004), I only caught 1 individual *Lasioglossum* specimen. Apidae includes some of the most important natural and agricultural pollinators such as the Western honey bee (*Apis mellifera*) and the common eastern bumblebee (*Bombus impatiens*), both of which were collected (Schemske et al. 1978). Despite *Apis mellifera* being a nonnative species brought to North America by humans around the 1620s (Engel et al. 2009), it is an example of a naturalized pollinator that is important for pollinating both wildflowers and agricultural crops and has seen drastic declines in recent years (Paudel et al. 2015). Only 11 *Apis mellifera* were caught in my study, but it was present in stands of all burn frequencies and thinning statuses. Sphecidae was the second most abundant Hymenoptera family, and they are both pollinators themselves (Bohart and Nye 1960, Steiner et al. 2005) and parasitoids of other Hymenoptera pollinators (Dukas 2005). Ichneumonidae, the third most abundant Hymenoptera family, are also important pollinators (Brys et al. 2008, Pauw 2013) and parasitoids of Lepidoptera (Puttler 1961, Yang 1993). Lepidoptera, including moths, are an important and diverse family of pollinators in their own right (Macgregor et al. 2015). Insect pollinator communities are complex, and high abundances

of some pollinators may in turn be detrimental to other pollinators, making it difficult to assess what species composition is overall best for the ecosystem.

Diptera

The larvae of many Diptera families use trees as hosts (Teskey 1976), but Diptera biomass and abundance was lower when the density of trees was greater. This could be because some of the most abundant and largest Diptera individuals collected were horse flies (Family: Tabanidae), which rely on nectar from flowering plants and the blood of animals for food (Kniepert 1980). Lower tree densities could support greater amounts of ground vegetation by allowing more sunlight to reach the forest floor (McConnell and Smith 1970). These lower tree densities could also, as a result of thinning, provide better habitat for wildlife that act as bloodmeal hosts by allowing more ground vegetation for cover and food (Neill and Puettmann 2013). However, Diptera abundance did not show a relationship with forbs or grass, and Diptera biomass was marginally lower when there were more grass and forbs in competitive models. Diptera biomass and abundance were both greater when there was more woody vegetation, supporting the idea that Diptera distribution is related to cover for host animals. Total insect biomass was likely also lower with greater tree densities and greater with more woody vegetation due to Diptera, and especially heavy horse flies, making up most of the total insect biomass.

Coleoptera

Coleoptera abundance was negatively associated with basal area, which is consistent with previous findings in the Arkansas Ozarks (Blanco and Garrie 2020). This previous study used blacklight traps to collect Coleoptera. Since I used passive traps without attractant in this study, the relationship is indeed likely due to the vegetation

characteristics supporting more Coleoptera and not due to increased visual obstruction with greater basal area. This is also likely related to my findings that Coleoptera biomass increased with decreasing canopy cover. As basal area increases, the canopy cover generally also increases (Jennings et al. 1999). One hypothesis for the relationship between Coleoptera biomass and canopy cover is that decreased canopy cover results in increased ground vegetation that act as hosts for Coleoptera species (Hardee et al. 1999). However, increases in Coleoptera biomass were only associated with increases in bare ground in my study, and not with increases in ground vegetation. This could be because many Coleoptera overwinter in the soil, and overwintering Coleoptera can continue to emerge from the soil as late as August (Burgess 1977, Hardee et al. 1999), which was well into my field season. There may be a more direct explanation for the negative relationship between Coleoptera abundance and basal area. Some Coleoptera species show a preference for smaller trees (Weber and McPherson 1984), and some Coleoptera species have increased larval mortality in the bark of larger trees (Shibata et al. 1994). Both of these factors could contribute to Coleoptera being associated with smaller trees, and therefore associated with decreased basal area and canopy cover.

Lepidoptera

Similar to Coleoptera, Lepidoptera biomass was also greater in areas with more bare ground, which could be because Lepidoptera pupae also overwinter in the soil (Zheng et al. 2013, Spencer 2014). Bare ground was maximized in unthinned areas that received high burn frequencies, but burning can also result in the death of overwintering Lepidoptera pupae (Jiang et al. 2011). There was also lower Lepidoptera abundance when there was more litter, likely because litter was the most common groundcover type and

was essentially the inverse of vegetation. Lepidoptera as a whole have a wide variety of host plant types (Niemelä et al. 1982, Wiklund 1984, Ackery 1988, Spencer 2014, Leckie and Beadle 2018), so Lepidoptera abundance may be maximized by increasing ground vegetation in general and not just specific vegetation types. Likewise, there was a marginally greater Lepidoptera abundance with increasing tree density, which seems counterintuitive to the negative relationship between Lepidoptera biomass and tree density, basal area, and canopy cover. Greater tree densities may provide more hosts for smaller nocturnal Lepidoptera but reduce the abundance of ground vegetation hosts for larger diurnal Lepidoptera (Niemelä et al. 1982, Spencer 2014, Leckie and Beadle 2018). There could also be fewer small, nocturnal Lepidoptera with lower tree densities and basal area due to bats foraging in these open areas at night and reducing their numbers (Humes et al. 1999, Kalka et al. 2008, Williams-Guillén et al. 2008, Blanco and Garrie 2020). However, the relationships with basal area and tree density had small effect sizes and large standard errors for Lepidoptera biomass and abundance, indicating these may not be important patterns from a management perspective.

Hymenoptera

There was a greater Hymenoptera abundance and genus diversity with decreased canopy cover and decreased litter, consistent with findings that canopy thinning increases bee diversity and abundance, particularly with Halictidae spp. (Taki et al. 2010, Odanaka et al. 2020). This is likely the result of reductions in canopy cover and ground litter increasing ground vegetation (Wang et al. 2005). Grass is one of the vegetation types that increases with decreased canopy cover (McConnell and Smith 1970), and it was associated with greater Hymenoptera biomass. Grass could increase Hymenoptera

biomass due to the specific Hymenoptera families that I caught the most of using grasses for various ecological reasons. For example, members of the family Halictidae feed on grass pollen (Immelman and Eardley 2008), members of the family Sphecidae collect grass to build their nests (Evans 1982, O'Neill and O'Neill 2003), and members of the family Ichneumonidae have been found to be associated with grasses, likely due to it providing habitat for the insects they parasitize (Dawah and Rothfritz 1995). The greater Hymenoptera genus diversity with increased woody vegetation could be explained by the fact that Hymenoptera have been found to be associated with saplings (Jokimäki et al. 1998), and bees are pollinators of woody plants (Oliveira and Gibbs 2000). Although the top models are different, maximizing ground vegetation seems like an ideal strategy for managing for aerial Hymenoptera. Grass and woody vegetation seem to be more important than forbs and were both more prevalent in thinned areas compared to unthinned areas, suggesting thinning may be beneficial to Hymenoptera conservation.

Conclusions

Consistent with Hymenoptera abundance and Lepidoptera biomass, overall insect family diversity and Hymenoptera genus diversity were highest with decreased canopy cover and decreased litter, both of which were minimized with increased burn frequencies and thinning. These areas that received high burn frequencies combined with thinning also had the lowest tree densities and litter and the highest amount of grass, which were vegetation characteristics associated with a greater Lepidoptera species diversity. This is inconsistent with the intermediate disturbance hypothesis (Connell 1978, Sousa 1979), but it is consistent with findings that suggest that high disturbance is associated with greater insect diversity in pine savannas (Nighohossian 2014). The

intermediate disturbance hypothesis is not a universal rule, and there are actually more studies that show a monotonic increase in diversity with increasing disturbance (Mackey and Currie 2001). Consistent with this pattern, Hymenoptera species richness increases with larger clearcuts (Rubene et al. 2015), but many Lepidoptera rely on trees in their larval stage (Butler and Strazanac 2000, Spencer 2014). Thinning can increase (Taki et al. 2010) or decrease (Hill et al. 1995) butterfly richness and abundance. If Lepidoptera species diversity follows the intermediate disturbance hypothesis (Connell 1978, Sousa 1979), there could be a decrease in Lepidoptera species diversity when there are no or few trees present (Burford et al. 1999, Summerville 2011, Summerville et al. 2013).

Thinning could represent an intermediate intensity of disturbance that maximizes Lepidoptera species diversity (Intachat et al. 1997, Fermon et al. 2000, Thomas 2002). In my study, there was a greater Lepidoptera species diversity when there was a lower tree density, but there were no stands represented that received clearcuts or shelterwood harvests where most the trees were removed. Thinning fewer trees so that a stand resembles a woodland rather than a savanna may be the best strategy for maximizing pollinator biomass, abundance, and diversity, which could be a good indicators of forest health (Wang et al. 2008). However, there was not a broad enough range of disturbance or tree densities in my data to draw firm conclusions regarding the relationship between disturbance and insect diversity, and high intensity logging could increase overall pollinator abundance and diversity (Korpela et al. 2015). While there is evidence that pollinators and plants pollinated by insects are declining concurrently (Biesmeijer et al. 2006), efforts should be made to manage for insects and the plants they pollinate and rely on for food to sustain their symbiosis and therefore sustain the ecosystem as a whole.

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Table 1. Breakdown of the 30 sampled stands by treatment in last 12 years. Insects collected March-November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

	Burned x0	Burned x1–3	Burned x4
Not Thinned	6 stands	6 Stands	6 Stands
Thinned	0 stands	6 Stands	6 Stands

Table 2. Candidate model set for variables (in addition to month as a fixed effect and stand as a random effect) predicting insect biomass, abundance, and diversity. Models with lowest AICc chosen as top models for each dependent variable. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

All possible Responses	All Possible Models
	burn
Biomass:	thin
Total Insect Biomass	burn+thin
Coleoptera Biomass	burn*thin
Lepidoptera Biomass	burn+tempow thin+tempow
Abundance:	burn+thin+tempow
Coleoptera Abundance	burn*thin+tempow
Macroheterocera Abundance	burn+moon
Geometridae Abundance	thin+moon
Noctuidae Abundance	burn+thin+moon
Erebidae Abundance	burn*thin+moon
Notodontidae Abundance	burn+tempow+moon
Saturniidae Abundance	thin+tempow+moon burn+thin+tempow+moon
Diversity:	burn*thin+tempow+moon
Macroheterocera Family Diversity	tempow+moon
Erebidae Species Diversity	tempow
Notodontidae Species Diversity	moon
Saturnidae Species Diversity	Null model

Table 3. Candidate model set for variables predicting tree and groundcover vegetation.

Models with lowest AICc chosen as top models for each dependent variable. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

All possible Responses	All Possible Models
Canopy Cover (%)	burn
Basal Area (m ² /ha)	thin
Tree Density	burn+thin
Grass (%)	burn*thin
Forbs (%)	Null model

Table 4. Total numbers, mean numbers (\pm SE) per trap, total biomass, and mean biomass (\pm SE) per trap of all insect orders collected in blacklight traps throughout the study.

Lepidoptera numbers only include Macroheterocera specimens, but biomass includes Microlepidoptera. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Order	Total Number	Mean Number Per Trap	Total Biomass (g)	Mean Biomass Per Trap (g)
Lepidoptera	19,458	83.51 \pm 7.00	985.76	4.23 \pm 0.40
Coleoptera	10,111	43.39 \pm 4.13	2.03	2.03 \pm 0.17
Hymenoptera	983	4.22 \pm 2.16	9.63	0.04 \pm 0.02
Diptera	944	4.05 \pm 0.69	6.58	0.03 \pm 0.004
Hemiptera	547	2.35 \pm 0.56	17.1	0.07 \pm 0.01
Trichoptera	371	1.59 \pm 0.31	8.12	0.04 \pm 0.007
Neuroptera	283	1.21 \pm 0.22	25.13	0.11 \pm 0.02
Blattodea	186	0.80 \pm 0.16	2.86	0.01 \pm 0.002
Orthoptera	85	0.36 \pm 0.09	21.32	0.09 \pm 0.02
Mecoptera	66	0.28 \pm 0.17	0.45	0.002 \pm 0.001
Mantodea	33	0.14 \pm 0.07	1.19	0.01 \pm 0.002
Odonata	3	0.01 \pm 0.007	0.74	0.003 \pm 0.002
Total	33,070		1080.91	

Table 5. Relationships between each fixed effect and each response variable in the top model and models within ≤ 2.00 AICc of the top model. Up arrows (\uparrow) indicate a positive relationship and down arrows (\downarrow) indicate a negative relationship. Double arrows indicate the burn treatment effect is greater ($\uparrow\uparrow$) or lower ($\downarrow\downarrow$) than the other burn treatment. Asterisks (*) indicate that the standard error (SE) does not overlap with 0 and is less than the absolute value of the estimate (β) for that particular fixed effect. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Dependent Variable	Thin (Yes)	Burn x1–3 per 12 yr.	Burn x4 per 12 yr.	Temp. (° C)	Moon (%)
Total Insect Biomass	\downarrow^*			\uparrow^*	\downarrow^*
Coleoptera Biomass	\uparrow			\uparrow	\downarrow^*
Coleoptera Abundance		\uparrow	$\uparrow\uparrow^*$		\downarrow^*
Lepidoptera Biomass	\downarrow^*			\uparrow^*	\downarrow^*
Macroheterocera Abundance	\downarrow^*			\uparrow^*	\downarrow^*
Macroheterocera Family Diversity		$\downarrow\downarrow$	\downarrow	\uparrow^*	\downarrow
Geometridae Abundance	\downarrow^*			\uparrow^*	\uparrow
Noctuidae Abundance		\uparrow	\downarrow^*	\uparrow^*	\downarrow^*
Erebidae Abundance	\downarrow^*			\uparrow	\downarrow^*
Erebidae Species Diversity	\uparrow	\downarrow	\uparrow	\uparrow^*	
Notodontidae Abundance				\uparrow	\downarrow
Notodontidae Species Diversity	\downarrow	\downarrow^*	\uparrow^*		\uparrow^*
Saturniidae Abundance	\downarrow^*	\downarrow	$\downarrow\downarrow^*$	\uparrow^*	\uparrow^*
Saturnidae Species Diversity	\downarrow			\uparrow	\downarrow
Canopy Cover (%)	\downarrow^*			N/A	N/A
Basal Area (m ² /ha)	\downarrow^*	\downarrow^*	\downarrow^*	N/A	N/A
Tree Density	\downarrow^*			N/A	N/A
Grass (%)	\uparrow^*	\downarrow	\uparrow^*	N/A	N/A
Forbs (%)	\uparrow^*	\uparrow^*	\uparrow^*	N/A	N/A

Table 6. Top 5 models with the lowest AICc and the null model from multi-model selection process for total insect biomass, Coleoptera biomass, and Coleoptera abundance in blacklight traps. Model parameters included month as a fixed effect and stand as a random effect. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Rank	Model Parameters	K	ΔAICc	ω_i	LL
Total Insect Biomass					
1	thin+templo+moon	13	0.00	0.40	−684.11
2	templo+moon	12	0.05	0.39	−685.26
3	burn+templo+moon	14	3.81	0.06	−684.89
4	burn+thin+templo+moon	15	4.28	0.05	−683.98
5	burn*thin+templo+moon	16	5.45	0.03	−683.41
16	Null model	10	30.89	0.00	−702.90
Coleoptera Biomass					
1	moon	11	0.00	0.33	−454.74
2	templo+moon	12	1.28	0.18	−454.27
3	thin+moon	12	1.38	0.17	−454.32
4	burn+moon	13	2.37	0.10	−453.69
5	thin+templo+moon	13	2.63	0.09	−453.82
16	Null model	10	3.76	0.00	−465.22
Coleoptera Abundance					
1	burn+moon	13	0.00	0.50	−1221.83
2	burn+thin+moon	14	2.14	0.17	−1221.76
3	burn+templo+moon	14	2.18	0.17	−1221.78
4	burn+thin+templo+moon	15	4.33	0.06	−1221.72
5	burn*thin+moon	15	4.40	0.05	−1221.75
19	Null model	10	27.57	0.00	−1238.95

Table 7. Total numbers, mean numbers (\pm SE), and percent of total identified for all Macroheterocera families collected in blacklight traps throughout the study. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

	Family	Total Abundance	Mean Number Per Trap	% of Total
1	Noctuidae	4,617	19.82 ± 1.89	31.35
2	Geometridae	4,118	17.67 ± 1.98	27.96
3	Erebidae	2,750	11.8 ± 1.16	18.67
4	Notodontidae	1,422	6.13 ± 0.79	9.66
5	Saturniidae	1,352	5.80 ± 1.62	9.18
6	Lasiocampidae	345	1.48 ± 0.59	2.34
7	Sphingidae	86	0.63 ± 0.07	0.58
8	Apatelodidae	28	0.12 ± 0.04	0.19
9	Drepanidae	8	0.03 ± 0.01	0.05
10	Mimallonidae	2	0.009 ± 0.006	0.01
	Total	14,728		

Table 8. Total number of all Erebidae, Notodontidae, and Saturniidae species identified.

Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren

Counties, Arkansas.

Taxa	Total	Taxa	Total
Erebidae:	2911	Notodontidae:	1395
<i>Allotria elonympha</i>	47	<i>Datana integerrima</i>	91
<i>Anomis erosa</i>	1	<i>Datana major</i>	12
<i>Antheraea polyphemus</i>	1	<i>Datana perspicua</i>	297
<i>Anticarsia gemmatalis</i>	1	<i>Furcula borealis</i>	1
<i>Apantesis nais</i>	15	<i>Heterocampa obliqua</i>	95
<i>Apantesis phalerata</i>	5	<i>Heterocampa umbrata</i>	21
<i>Apantesis vittata</i>	14	<i>Hyparpax aurora</i>	2
<i>Argyrostromis anilis</i>	4	<i>Lochmaeus manteo</i>	3
<i>Bleptina caradrinalis</i>	4	<i>Nadata gibbosa</i>	297
<i>Caenurgia chloropha</i>	6	<i>Nerice bidentata</i>	3
<i>Caenurgina erechtea</i>	1	<i>Paraeschra georgica</i>	2
<i>Catocala flebilis</i>	2	<i>Peridea basitriens</i>	1
<i>Catocala ilia</i>	47	<i>Peridea ferruginea</i>	1
<i>Catocala innubens</i>	2	<i>Schizura ipomoeae</i>	1
<i>Catocala lacrymosa</i>	1	<i>Schizura leptinoides</i>	1
<i>Catocala neogama</i>	1	<i>Symmerista albifrons</i>	1
<i>Catocala piatrix</i>	1	Unknown Notodontidae	566
<i>Catocala ultronia</i>	6		
<i>Catocala umbrosa</i>	1	Saturniidae:	1102
<i>Catocala verrilliana</i>	1	<i>Actias luna</i>	113
<i>Catocala vidua</i>	8	<i>Anisota stigma</i>	10
<i>Celiptera frustulum</i>	21	<i>Antheraea polyphemus</i>	3
<i>Cisseps fulvicollis</i>	1	<i>Automeris io</i>	26
<i>Cisthene packardii</i>	24	<i>Citheronia regalis</i>	2
<i>Cisthene plumbea</i>	452	<i>Dryocampa rubicunda</i>	890
<i>Cisthene tenuifascia</i>	1	<i>Eacles imperialis</i>	57
<i>Clemensia albata</i>	17	Unknown Saturniidae	1
<i>Colobochyla interpuncta</i>	11		
<i>Crambidia pallida</i>	1		
<i>Dasychira manto</i>	3		
<i>Drasteria grandirena</i>	1		
<i>Euerythra phasma</i>	4		
<i>Euparthenos nubilis</i>	2		
<i>Gondysia smithii</i>	1		

<i>Grammia anna</i>	2
<i>Grammia figurata</i>	11
<i>Grammia parthenice</i>	9
<i>Grammia virgo</i>	3
<i>Halysidota tessellaris</i>	392
<i>Haploa clymene</i>	68
<i>Haploa contigua</i>	30
<i>Hemeroplanis scopulepes</i>	15
<i>Hyphantria cunea</i>	9
<i>Hypercompe scribonia</i>	8
<i>Hypoprepia fucosa</i>	450
<i>Hypoprepia miniata</i>	147
<i>Hypsoropha hormos</i>	1
<i>Hypsoropha monilis</i>	1
<i>Idia rotundalis</i>	23
<i>Lycomorpha pholus</i>	3
<i>Mocis latipes</i>	24
<i>Mocis texana</i>	45
<i>Orgyia leucostigma</i>	1
<i>Pagara simplex</i>	1
<i>Panopoda carneicosta</i>	7
<i>Panopoda rufimargo</i>	4
<i>Parallelia bistriaris</i>	30
<i>Phoberia atomaris</i>	1
<i>Phyprosopus callitrichoides</i>	3
<i>Phytometra rhodarialis</i>	1
<i>Renia adspersgillus</i>	1
<i>Renia fraternalis</i>	1
<i>Rivula propinquialis</i>	1
<i>Rivula sericealis</i>	1
<i>Scolecocampa liburna</i>	7
<i>Spilarctia luteum</i>	1
<i>Spiloloma lunilinea</i>	1
<i>Spilosoma congrua</i>	176
<i>Spilosoma virginica</i>	7
<i>Virbia aurantiaca</i>	307
<i>Virbia laeta</i>	9
<i>Virbia opella</i>	46
<i>Zale horrida</i>	4
<i>Zale lunata</i>	3
<i>Zale metatoides</i>	2

<i>Zale obliqua</i>	15
<i>Zale unilineata</i>	19
<i>Zanclognatha martha</i>	8
Unknown Erebidæ	305

Table 9. Top 5 models with the lowest AICc and the null model from multi-model selection process for Lepidoptera biomass, Macroheterocera Abundance, and Macroheterocera Family Diversity in blacklight traps. Model parameters included month as a fixed effect and stand as a random effect. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Rank	Model Parameters	K	ΔAICc	ω_i	LL
Lepidoptera Biomass					
1	thin+templo	12	0.00	0.25	−657.94
2	thin+templo+moon	13	0.09	0.24	−656.86
3	templo	11	1.29	0.13	−659.69
4	templo+moon	12	1.36	0.13	−658.62
5	burn+thin+templo+moon	15	3.57	0.04	−656.33
17	Null model	10	14.36	0.00	−667.33
Macroheterocera Abundance					
1	thin+templo	12	0.00	0.23	−1340.35
2	thin+templo+moon	13	0.26	0.20	−1339.36
3	templo	11	1.22	0.12	−1342.07
4	templo+moon	12	1.43	0.11	−1341.07
5	burn*thin+templo	15	2.45	0.07	−1338.18
17	Null model	10	18.80	0.00	−1351.97
Macroheterocera Family Diversity					
1	templo	11	0.00	0.36	105.48
2	burn+templo	13	1.77	0.15	106.83
3	templo+moon	12	1.92	0.14	105.64
4	thin+templo	12	2.08	0.13	105.56
5	burn+templo+moon	14	3.82	0.05	106.94
16	Null model	10	44.06	0.00	82.35

Table 10. Top 5 models with the lowest AICc and the null model from the multi-model selection process for Geometridae abundance and Noctuidae abundance in blacklight traps. Model parameters included month as a fixed effect and stand as a random effect. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Rank	Model Parameters	K	ΔAICc	ω_i	LL
Geometridae Abundance					
1	thin+tempow	12	0.00	0.29	−1086.61
2	tempow	11	0.76	0.20	−1088.10
3	thin+tempow+moon	13	2.00	0.11	−1086.49
4	tempow+moon	12	2.75	0.07	−1087.99
5	burn+thin+tempow	14	3.50	0.05	−1086.11
9	Null model	10	4.76	0.03	−1091.21
Noctuidae Abundance					
1	tempow	11	0.00	0.25	−1063.51
2	tempow+moon	12	1.00	0.15	−1062.90
3	burn+tempow	13	1.35	0.13	−1062.95
4	burn+tempow+moon	14	2.04	0.09	−1061.16
5	thin+tempow	12	2.08	0.09	−1063.44
16	Null model	10	12.31	0.00	−1070.77

Table 11. Top 5 models with the lowest AICc and the null model from multi-model selection process for Erebidae abundance, Notodontidae abundance, and Saturniidae abundance in blacklight traps. Model parameters included month as a fixed effect and stand as a random effect. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Rank	Model Parameters	K	ΔAICc	ω_i	LL
Erebidae Abundance					
1	Null model	10	0.00	0.17	−929.29
2	moon	11	0.36	0.14	−928.37
3	thin	11	0.39	0.14	−928.38
4	thin+moon	12	0.77	0.12	−927.46
5	templow	11	1.57	0.08	−928.97
6	thin+templow	12	1.99	0.06	−928.07
Notodontidae Abundance					
1	Null model	10	0.00	0.32	−845.71
2	templow	11	1.70	0.14	−845.46
3	moon	11	1.86	0.13	−845.54
4	thin	11	2.01	0.12	−845.62
5	thin+templow	12	3.73	0.05	−845.36
6	templow+moon	12	3.83	0.05	−845.43
Saturniidae Abundance					
1	burn+templow+moon	14	0.00	0.31	−1049.43
2	templow+moon	12	0.77	0.21	−1052.07
3	thin+templow+moon	13	1.53	0.14	−1051.33
4	burn+thin+templow+moon	15	1.95	0.12	−1049.26
5	burn+templow	13	3.56	0.05	−1052.34
11	Null model	10	7.26	0.01	−1057.53

Table 12. Top 5 models with the lowest AICc and the null model from multi-model selection process for Erebidæ species diversity, Notodontidæ species diversity, and Saturniidæ species diversity in blacklight traps. Model parameters included month as a fixed effect and stand as a random effect. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Rank	Model Parameters	K	ΔAICc	ω_i	LL
Erebidæ Species Diversity					
1	Null model	10	0.00	0.17	25.25
2	templow	11	0.53	0.13	26.09
3	burn	12	0.95	0.11	26.99
4	thin	11	1.49	0.08	25.61
5	burn+templow	13	1.98	0.06	27.60
6	thin+templow	12	2.01	0.06	26.46
Notodontidæ Species Diversity					
1	burn*thin+moon	15	0.00	0.31	61.07
2	moon	11	1.49	0.15	55.82
3	burn+moon	13	2.17	0.10	57.71
4	burn*thin+templow+moon	16	2.23	0.10	61.11
5	thin+moon	12	3.11	0.07	56.12
12	Null model	10	5.91	0.02	52.51
Saturniidæ Species Diversity					
1	Null model	10	0.00	0.26	133.08
2	templow	11	1.12	0.15	133.63
3	moon	11	1.43	0.13	133.47
4	thin	11	1.45	0.13	133.46
5	thin+templow	12	2.60	0.07	134.00
6	thin+moon	12	2.87	0.06	133.86

Table 13. Top 5 models with the lowest AICc and the null model from multi-model selection process for canopy cover, basal area, tree density, grass, and forbs. Model parameters included month as a fixed effect and stand as a random effect. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Rank	Model Parameters	K	ΔAICc	ω_i	LL
Canopy Cover (%)					
1	thin	11	0.00	0.66	−869.42
2	burn+thin	13	2.21	0.22	−868.29
3	burn*thin	14	4.37	0.07	−868.24
4	burn	12	6.48	0.03	−871.55
5	Null model	10	6.57	0.02	−873.81
Basal Area (m²/ha)					
1	thin	11	0.00	0.40	−883.45
2	burn+thin	13	1.10	0.23	−881.76
3	burn	12	1.47	0.19	−883.07
4	burn*thin	14	2.81	0.10	−881.48
5	Null model	10	3.35	0.08	−886.23
Tree Density					
1	thin	11	0.00	0.62	−849.02
2	burn+thin	13	2.96	0.14	−848.26
3	burn*thin	14	3.91	0.09	−847.61
4	Null model	10	4.12	0.08	−852.18
5	burn	12	4.38	0.07	−850.10
Grass (%)					
1	burn+thin	13	0.00	0.57	−906.16
2	burn*thin	14	2.26	0.19	−906.16
3	thin	11	2.83	0.14	−909.81
4	burn	12	3.69	0.09	−909.13
5	Null model	10	8.07	0.01	−913.53
Forbs (%)					
1	thin	11	0.00	0.35	−899.14
2	burn+thin	13	0.04	0.35	−896.93
3	burn*thin	14	1.01	0.21	−896.28
4	burn	12	3.10	0.08	−899.58
5	Null model	10	6.98	0.01	−903.74

Table 14. Candidate model set for variables (in addition to month as a fixed effect and stand as a random effect) predicting insect biomass, abundance, and diversity. Models with lowest AICc chosen as top models for each dependent variable. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

All possible Responses	All Possible Models
	canopy+grass
	canopy+forb
Biomass:	canopy+litter
Total Biomass	canopy+bare
Coleoptera Biomass	canopy+woody
Lepidoptera Biomass	basal+grass
Hymenoptera Biomass	basal+forb
Diptera Biomass	basal+litter
	basal+bare
	basal+woody
Abundance:	tree+grass
Diptera Abundance	tree+forb
Coleoptera Abundance	tree+litter
Lepidoptera Abundance	tree+bare
Hymenoptera Abundance	tree+woody
	grass
	forb
	litter
Diversity:	bare
Insect Family Diversity	woody
Lepidoptera Species Diversity	canopy
Hymenoptera Genus Diversity	basal
	tree
	Null model

Table 15. Total numbers, mean numbers (\pm SE) per trap, total biomass, and mean biomass (\pm SE) per trap of all insect orders collected in malaise traps throughout the study. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Order	Total Number	Mean Number Per Trap	Total Biomass (g)	Mean Biomass Per Trap (g)
Diptera	7,221	32.38 ± 2.35	146.41	0.65 ± 0.09
Lepidoptera	973	6.16 ± 0.46	24.02	0.14 ± 0.01
Hymenoptera	747	4.96 ± 0.0004	8.26	0.05 ± 0.005
Coleoptera	282	3.44 ± 0.58	3.44	0.11 ± 0.007
Hemiptera	61	1.24 ± 0.04	0.66	0.01 ± 0.0006
Orthoptera	20	1.05 ± 0.01	5.37	0.23 ± 0.01
Odonata	10	1.67 ± 0.05	0.13	0.01 ± 0.0004
Blattodea	3	1.50 ± 0.05	0.03	0.03 ± 0.00
Mecoptera	2	1 ± 0.00	0.02	0.01 ± 0.00
Phasmatodea	1	1 ± 0.00	0.21	0.21 ± 0.00
Plecoptera	1	1 ± 0.00	0.01	0.01 ± 0.00

Table 16. Relationships between each fixed effect and each response variable in the top model and models within ≤ 2.00 AICc of the top model. Up arrows (\uparrow) indicate a positive relationship and down arrows (\downarrow) indicate a negative relationship. Asterisks (*) indicate that the standard error (SE) does not overlap with 0 and is less than the absolute value of the estimate (β) for that particular fixed effect. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Dependent Variable	Canopy (%)	Basal (m²/ha)	Tree Density	Grass (%)	Forb (%)	Woody (%)	Litter (%)	Bare (%)
Total Biomass		\downarrow	\downarrow^*			\uparrow^*		\uparrow^*
Diptera Biomass		\downarrow	\downarrow	\downarrow	\downarrow	\uparrow^*		
Diptera Abundance			\downarrow^*			\uparrow		
Coleoptera Biomass	\downarrow^*							\uparrow^*
Coleoptera Abundance		\downarrow^*						\uparrow^*
Hymenoptera Biomass	\downarrow^*			\uparrow^*				
Hymenoptera Abundance	\downarrow^*					\uparrow^*	\downarrow^*	
Hymenoptera Genus Diversity	\downarrow^*					\uparrow^*	\downarrow^*	
Lepidoptera Biomass		\downarrow	\downarrow					\uparrow^*
Lepidoptera Abundance		\uparrow	\uparrow				\downarrow^*	
Lepidoptera Species Diversity		\downarrow^*	\downarrow^*	\uparrow^*			\downarrow^*	
Insect Family Diversity	\downarrow^*	\downarrow^*				\uparrow^*	\downarrow^*	

Table 17. Top 5 models with the lowest AICc and the null model from multi-model selection process for total insect biomass and insect family diversity in malaise traps. Model parameters included month as a fixed effect and stand as a random effect. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Rank	Model Parameters	K	ΔAICc	ω_i	LL
Total Insect Biomass					
1	tree	11	0.00	0.16	−339.83
2	tree+woody	12	0.36	0.13	−338.89
3	tree+bare	12	1.17	0.09	−339.30
4	basal+woody	12	1.41	0.08	−339.42
5	basal	11	1.57	0.07	−340.61
12	Null model	10	3.41	0.03	−342.63
Insect Family Diversity					
1	canopy+litter	12	0.00	0.17	−22.81
2	canopy+woody	12	0.70	0.12	−23.16
3	litter	11	0.84	0.11	−24.34
4	canopy	11	0.91	0.11	−24.38
5	basal+litter	12	1.17	0.09	−23.39
12	Null model	10	3.75	3.75	−26.89

Table 18. Top models with the lowest AICc and the null model from multi-model selection process for Diptera biomass, Diptera abundance, Coleoptera biomass, and Coleoptera abundance in malaise traps. Model parameters included month as a fixed effect and stand as a random effect. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Rank	Model Parameters	K	ΔAICc	ω_i	LL
Diptera Biomass					
1	tree	11	0.00	0.14	−329.62
2	tree+woody	12	0.04	0.14	−328.53
3	basal+woody	12	0.66	0.10	−328.83
4	basal	11	1.11	0.08	−330.17
5	tree+bare	12	1.13	0.06	−329.07
6	tree+forb	12	1.74	0.06	−329.37
7	tree+grass	12	1.92	0.05	−329.46
14	Null model	10	3.54	0.02	−332.49
Diptera Abundance					
1	tree	11	0.00	0.31	−1131.92
2	tree+woody	12	1.53	0.15	−1131.58
3	tree+grass	12	2.11	0.11	−1131.86
4	tree+litter	12	2.11	0.11	−1131.87
5	tree+forb	12	2.11	0.11	−1131.87
17	Null model	10	21.19	0.00	−1143.62
Coleoptera Biomass					
1	canopy+bare	12	0.00	0.49	306.34
2	canopy+grass	12	2.77	0.12	304.95
3	canopy	11	3.33	0.09	303.56
4	canopy+litter	12	3.37	0.09	304.65
5	canopy+woody	12	3.79	0.07	304.44
8	Null model	10	7.83	0.01	300.21
Coleoptera Abundance					
1	basal+bare	12	0.00	0.65	−726.09
2	tree+bare	12	1.88	0.25	−727.03
3	canopy+bare	12	5.13	0.05	−728.66
4	basal	11	8.22	0.01	−731.31
5	basal+grass	12	8.78	0.01	−730.71
20	Null model	10	20.34	0.00	−738.47

Table 19. Total numbers of Hymenoptera identified to species collected in malaise traps throughout study. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Species	Total
<i>Apis mellifera</i>	11
<i>Bombus impatiens</i>	7
<i>Ceratina calcarata</i>	7
<i>Ceratina dupla</i>	1
<i>Xylo virginica</i>	21
<i>Arge humeralis</i>	1
<i>Trypoxylon politum</i>	1
<i>Camponotus castaneus</i>	1
<i>Augochlorella persimilis</i>	2
<i>Lasioglossum creberrimum</i>	1
<i>Dolichomitrus irritator</i>	1
<i>Gnamptopelta obsidianator</i>	1
<i>Megarhyssa atrata</i>	1
<i>Megarhyssa greenei</i>	2
<i>Pristaulacus flavicrurus</i>	5
<i>Pimpla croceiventris</i>	1
<i>Dasymutilla quadriguttata</i>	22
<i>Onycholyda luteicornis</i>	2
<i>Auplopus mellipes</i>	1
<i>Priocnemis cornica</i>	2
<i>Priocnemis minorata</i>	4
<i>Ammophila nigricans</i>	1
<i>Ammophila procera</i>	3
<i>Eremnophila aureonotata</i>	7
<i>Macrophya formosa</i>	6
<i>Dolichovespula maculata</i>	8
<i>Monobia quadridens</i>	2
<i>Polistes carolina</i>	4
<i>Polistes metricus</i>	1
<i>Vespula consobrina</i>	1
<i>Vespula maculifrons</i>	17

Table 20. Top 5 models with the lowest AICc and the null model from the multi-model selection process for Hymenoptera biomass, Hymenoptera abundance, and Hymenoptera genus diversity in malaise traps. Model parameters included month as a fixed effect and stand as a random effect. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Rank	Model Parameters	K	ΔAICc	ω_i	LL
Hymenoptera Biomass					
1	canopy+grass	12	0.00	0.55	316.06
2	canopy	11	2.20	0.18	313.85
3	canopy+woody	12	4.08	0.07	314.02
4	canopy+litter	12	4.23	0.07	313.95
5	canopy+forb	12	4.37	0.06	313.88
17	Null model	10	53.03	0.00	287.34
Hymenoptera Abundance					
1	canopy+litter	12	0.00	0.37	−688.39
2	canopy+woody	12	1.88	0.14	−689.33
3	canopy	11	2.22	0.12	−690.61
4	basal+litter	12	2.69	0.10	−689.72
5	canopy+forb	12	2.97	0.08	−689.87
21	Null model	10	28.82	0.00	−705.00
Hymenoptera Genus Diversity					
1	canopy+woody	12	0.00	0.39	−15.47
2	canopy+litter	12	0.63	0.28	−15.78
3	canopy	11	2.54	0.11	−17.85
4	canopy+bare	12	3.54	0.07	−17.24
5	canopy+woody	12	3.99	0.05	−17.46
22	Null model	10	17.81	0.00	−26.58

Table 21. Total numbers of butterflies identified to species collected in malaise traps throughout study. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Taxa	Total
Hesperiidae	147
<i>Achalarus lyciades</i>	11
<i>Epargyreus clarus</i>	11
<i>Erynnis baptisiae</i>	3
<i>Erynnis brizo</i>	1
<i>Erynnis horatius</i>	8
<i>Erynnis juvenalis</i>	6
<i>Euphyes vestris</i>	37
<i>Hylephila phyleus</i>	11
<i>Poanes hobomok</i>	4
<i>Poanes viator</i>	1
<i>Poanes yehl</i>	1
<i>Thorybes bathyllus</i>	7
<i>Thorybes pylades</i>	47
<i>Udea rubigalis</i>	1
Lycaenidae	41
<i>Calycopis cecrops</i>	1
<i>Celastrina ladon</i>	3
<i>Cupido comyntas</i>	29
<i>Satyrium titus</i>	1
Nymphalidae	148
<i>Anaea andria</i>	1
<i>Cercyonis pegala</i>	2
<i>Cyllopsis gemma</i>	10
<i>Hermeuptychia sosybius</i>	2
<i>Junonia coenia</i>	1
<i>Libytheana carinenta</i>	1
<i>Limenitis arthemis</i>	3
<i>Megisto cymela</i>	32
<i>Phyciodes cocyta</i>	2
<i>Phyciodes tharos</i>	40
<i>Polygonia comma</i>	1
<i>Polygonia interrogationis</i>	4
<i>Speyeria cybele</i>	1
<i>Vanessa atalanta</i>	48

<i>Vanessa virginiensis</i>	2
Papilionidae	33
<i>Battus philenor</i>	25
<i>Eurytides marcellus</i>	2
<i>Papilio glaucus</i>	1
<i>Papilio troilus</i>	4
Pieridae	2
<i>Anthocharis midea</i>	1
<i>Pyrisitia lisa</i>	1
Zygaenoidae	1
Monoleuca	1
<i>Monoleuca semifascia</i>	1

Table 22. Top 5 models with the lowest AICc and the null model from multi-model selection process for Lepidoptera biomass, Lepidoptera abundance, and Lepidoptera species diversity in malaise traps. Model parameters included month as a fixed effect and stand as a random effect. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

Rank	Model Parameters	K	ΔAICc	ω_i	LL
Lepidoptera Biomass					
1	tree+bare	12	0.00	0.47	117.12
2	basal+bare	12	0.33	0.39	116.96
3	canopy+bare	12	3.98	0.06	115.13
4	bare	11	6.82	0.02	112.60
5	tree+woody	12	7.31	0.01	113.47
21	Null model	10	15.48	0.00	107.17
Lepidoptera Abundance					
1	tree+litter	12	0.00	0.42	−726.00
2	basal+litter	12	0.32	0.35	−726.16
3	tree+forb	12	3.70	0.07	−727.85
4	basal+forb	12	3.78	0.06	−727.89
5	tree	11	6.24	0.02	−730.23
21	Null model	10	22.11	0.00	−739.27
Lepidoptera Species Diversity					
1	basal+litter	12	0.00	0.29	−7.63
2	basal+grass	12	0.27	0.25	−7.77
3	tree+grass	12	0.67	0.21	−7.97
4	tree+litter	12	2.41	0.09	−8.84
5	canopy+litter	12	4.38	0.03	−9.83
21	Null model	10	11.81	0.00	−15.76

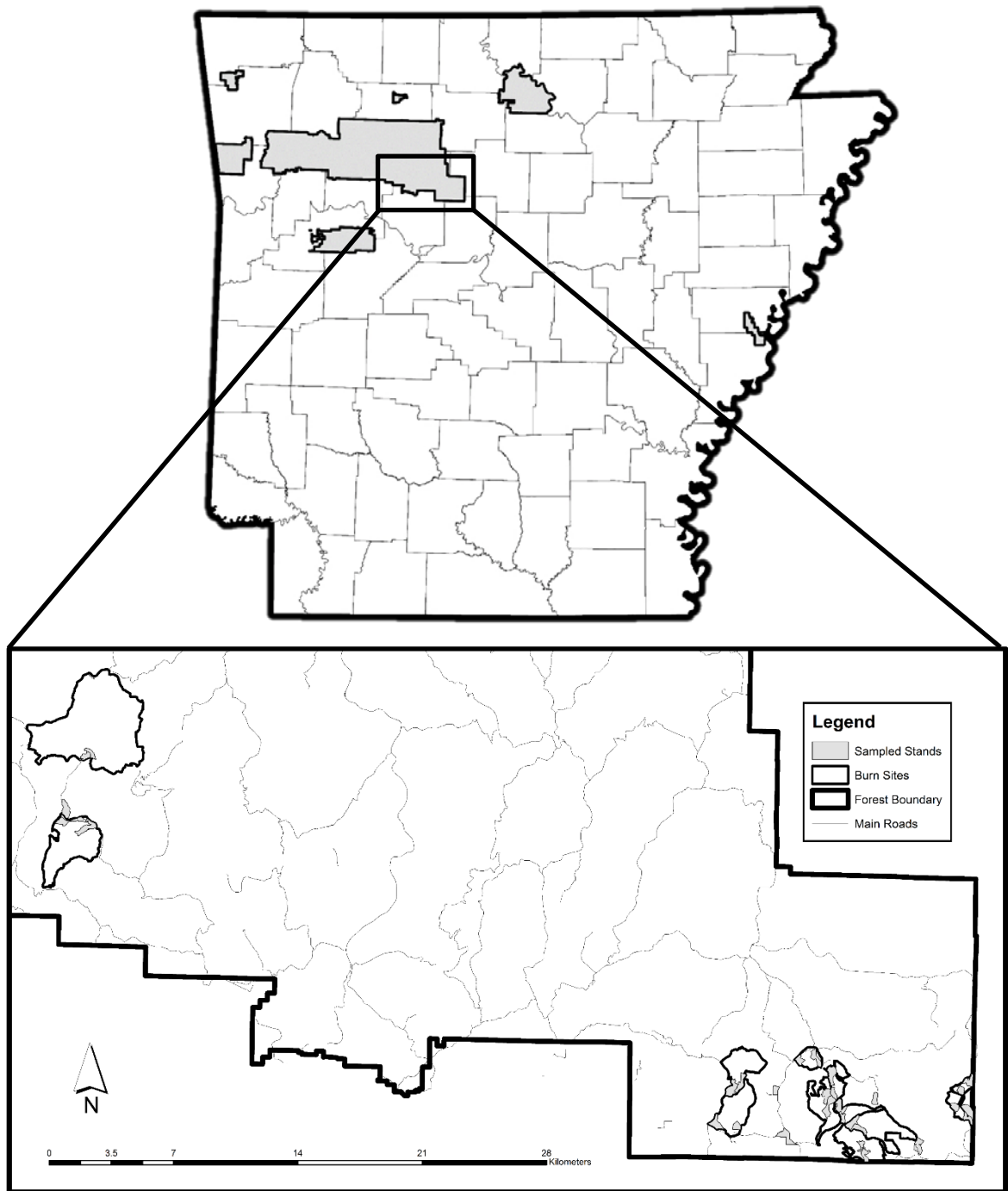


Figure 1. Map of study area and burn sites in the Big Piney Ranger District of the Ozark National Forest in Arkansas. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

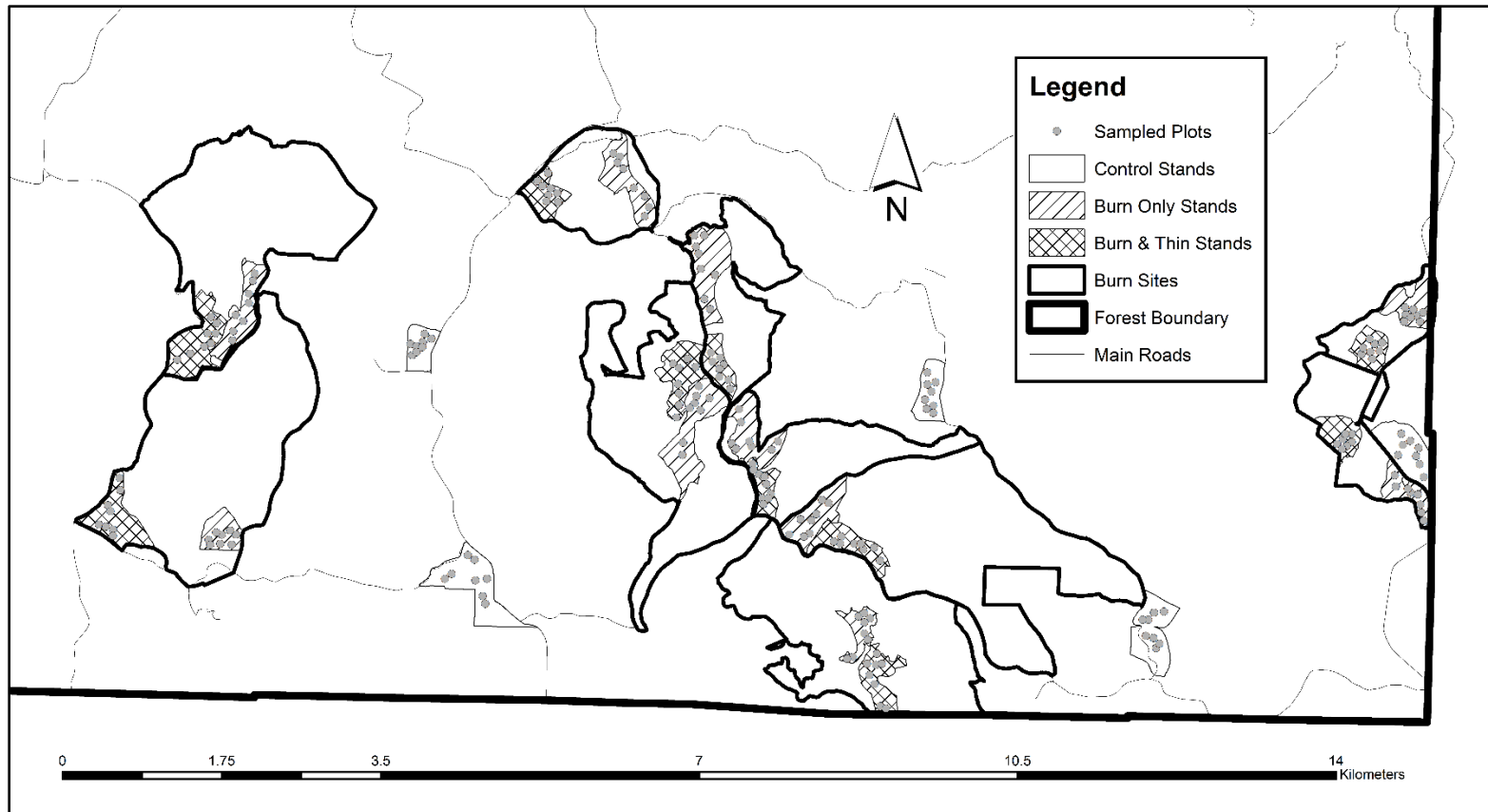


Figure 2. Example of burn-only and burn-thin stands within larger burn sites, as well as separate control stands. The points within the stands represent the randomly generated locations of the sampling plots. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

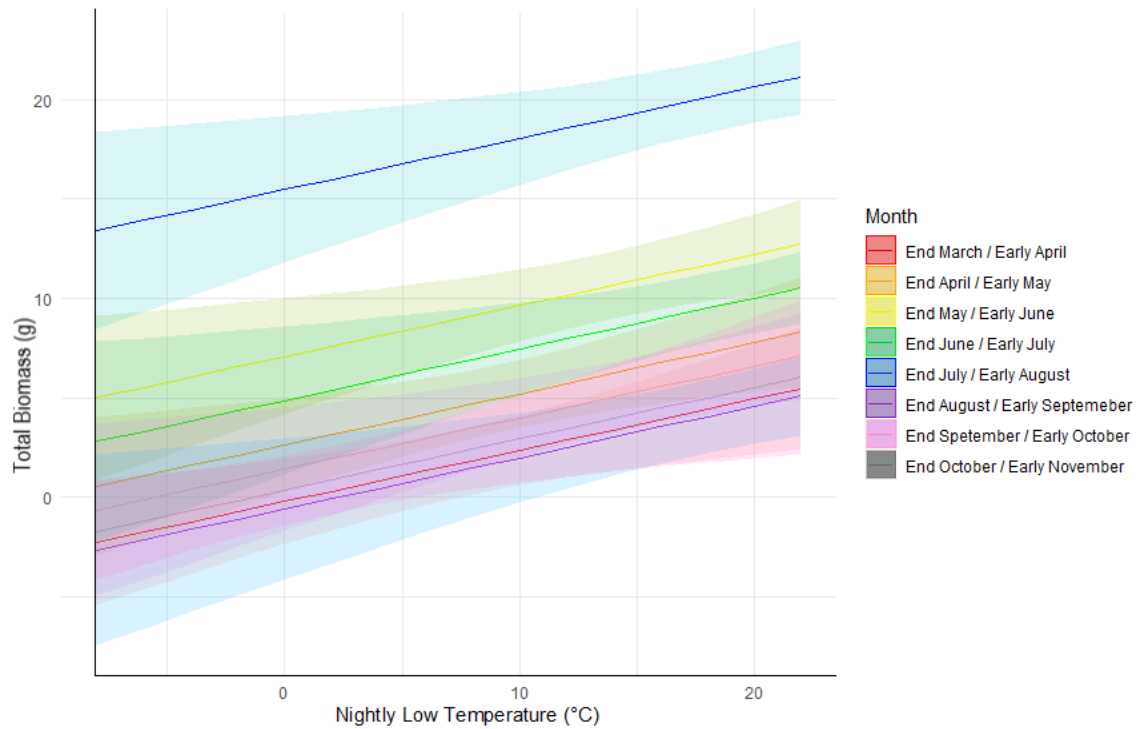


Figure 3. Predicted values ($\pm 95\%$ CI) for nightly low temperature in the top model for total insect biomass. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

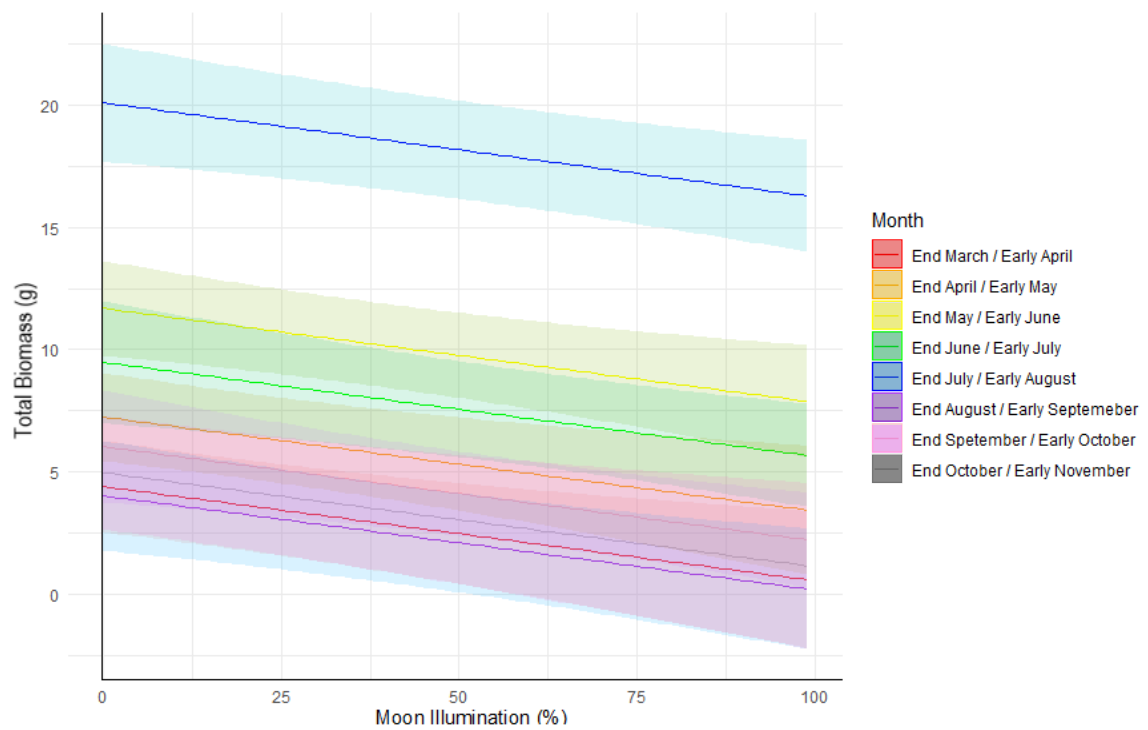


Figure 4. Predicted values ($\pm 95\%$ CI) for moon illumination in the top model for total insect biomass. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

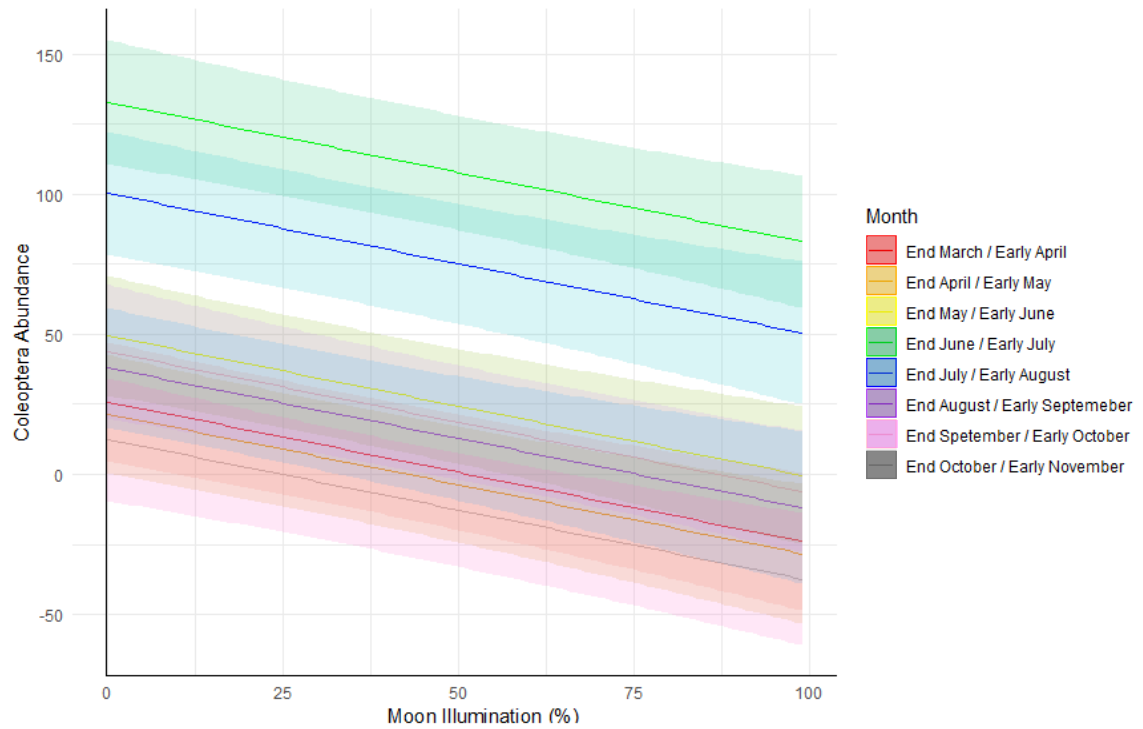


Figure 5. Predicted values ($\pm 95\%$ CI) for moon illumination in the top model for Coleoptera abundance. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

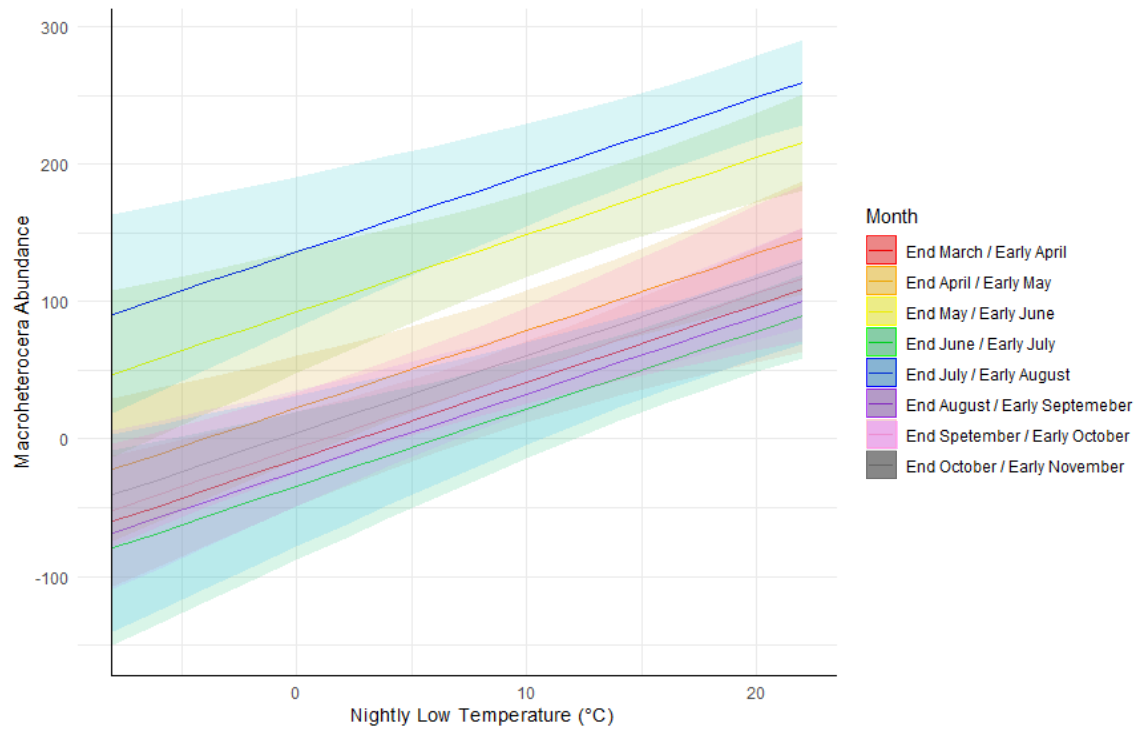


Figure 6. Predicted values ($\pm 95\%$ CI) for nightly low temperature in the top model for Macroheterocera abundance. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

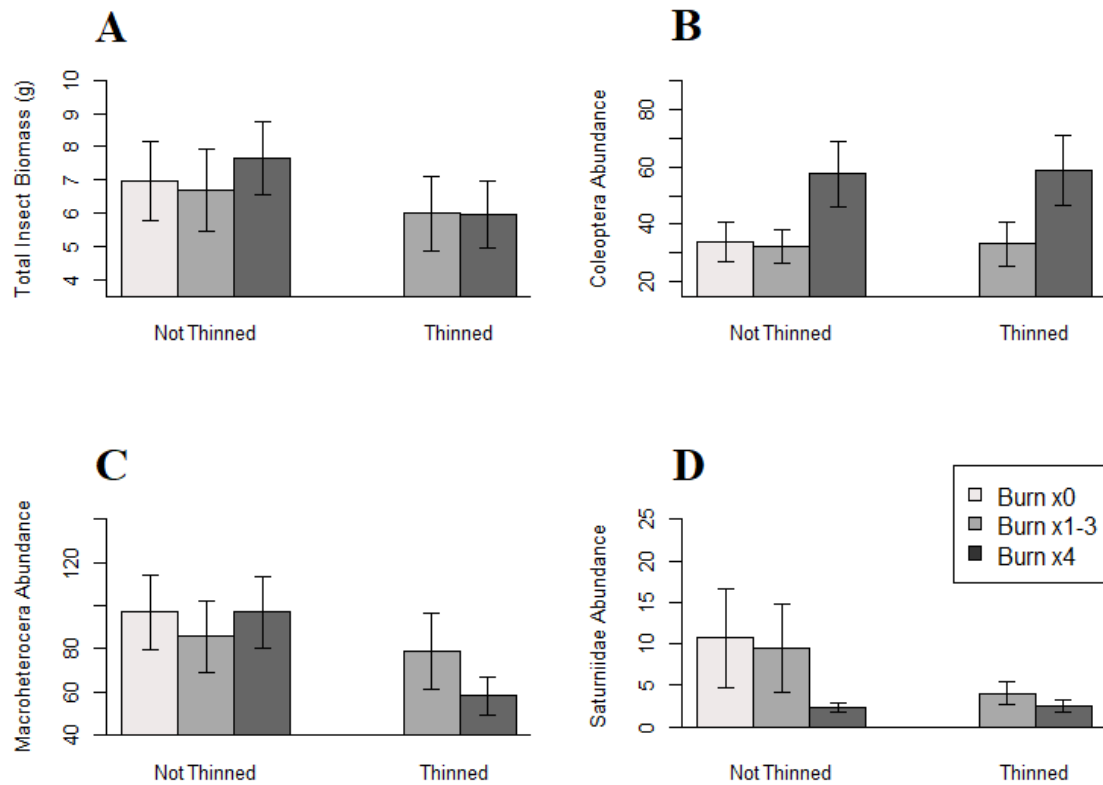


Figure 7. Mean ($\pm 95\%$ CI) total insect biomass (**A**), Coleoptera abundance (**B**), Macroheterocera abundance (**C**), and Saturniidae abundance (**D**) per sampling point for each burn frequency and thinning status. Pseudoreplication of the stands, seasonal differences, nightly low temperature ($^{\circ}\text{C}$), and moon illumination (%) are not taken into account. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

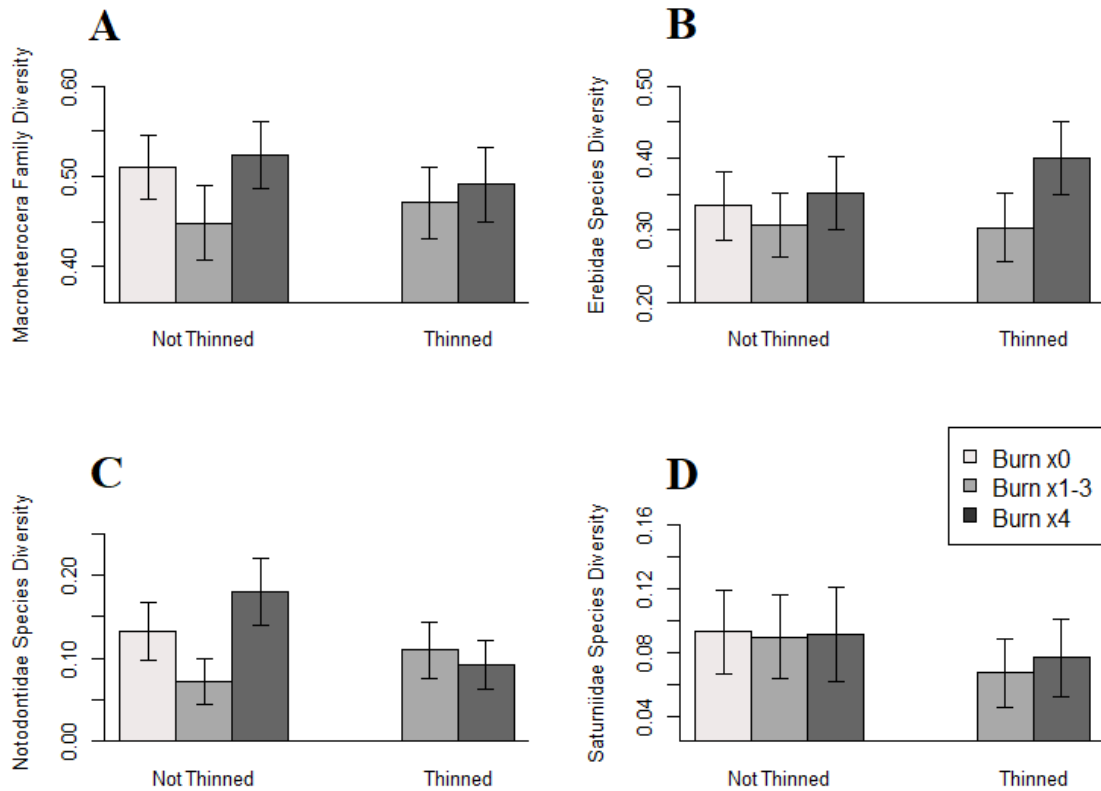


Figure 8. Mean diversity ($\pm 95\%$ CI) of Macroheterocera (**A**), Erebidæ (**B**), Notodontidæ (**C**), and Saturniidæ (**D**) per sampling point for each burn frequency and thinning status. Pseudoreplication of the stands, seasonal differences, nightly low temperature ($^{\circ}\text{C}$), and moon illumination (%) are not taken into account. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

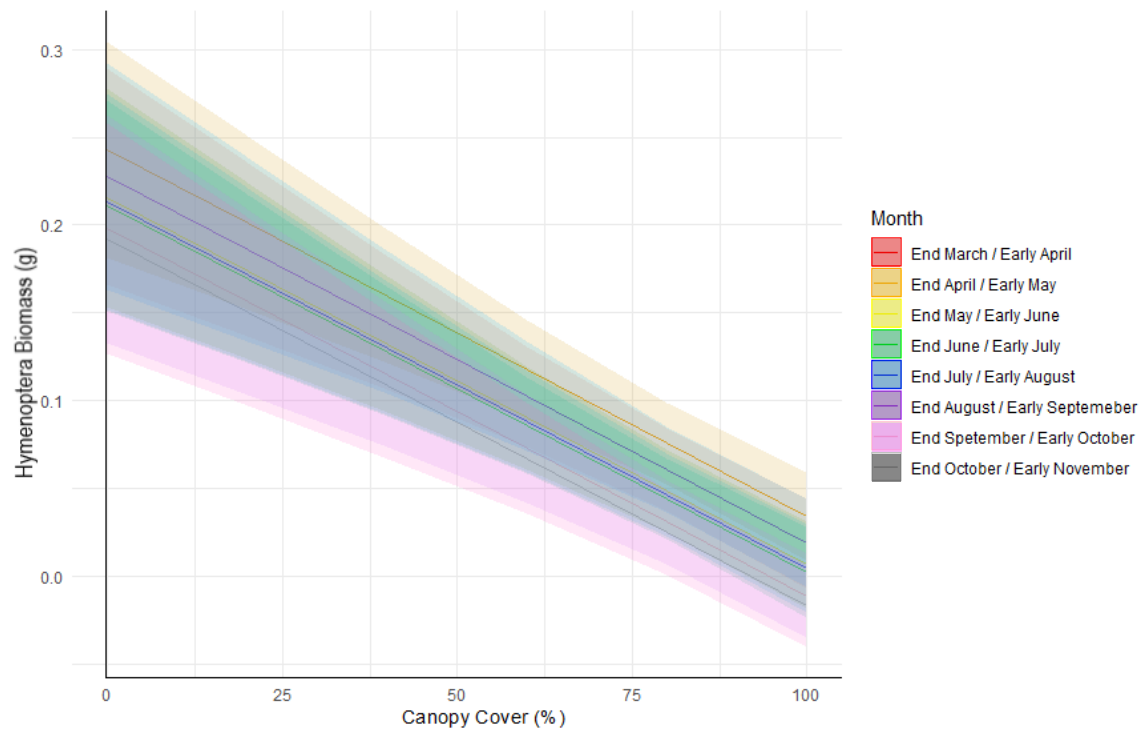


Figure 9. Predicted values ($\pm 95\%$ CI) for canopy cover in the top model for Hymenoptera biomass. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

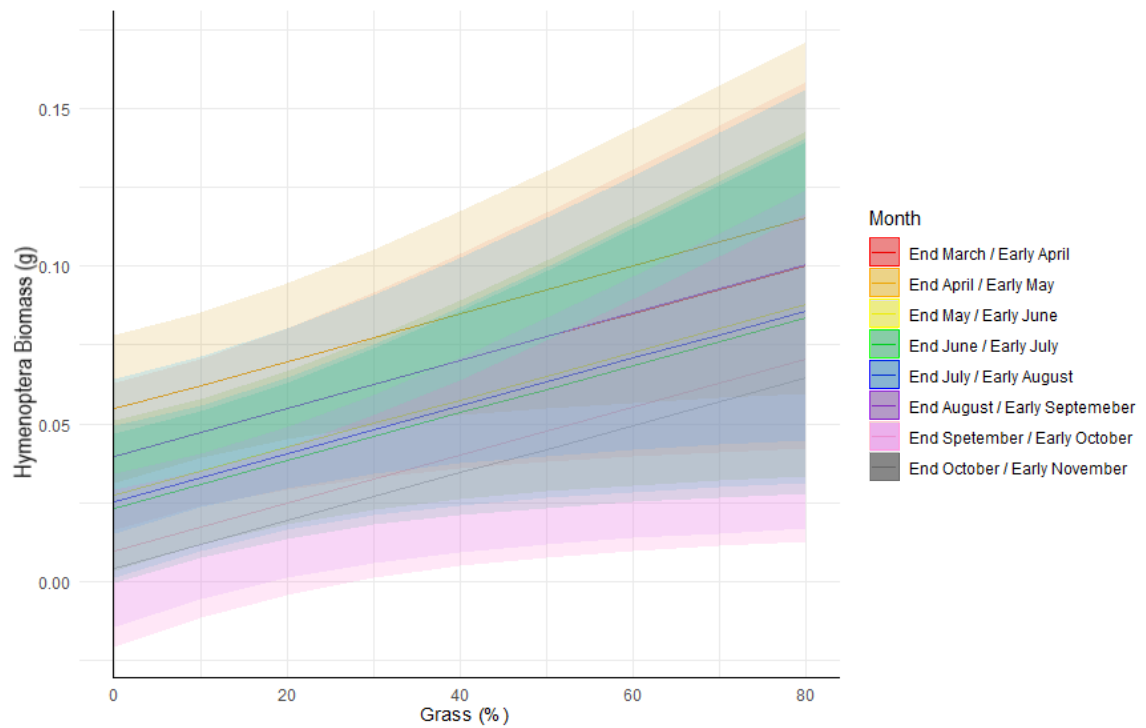


Figure 10. Predicted values ($\pm 95\%$ CI) for grass in the top model for Hymenoptera biomass. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

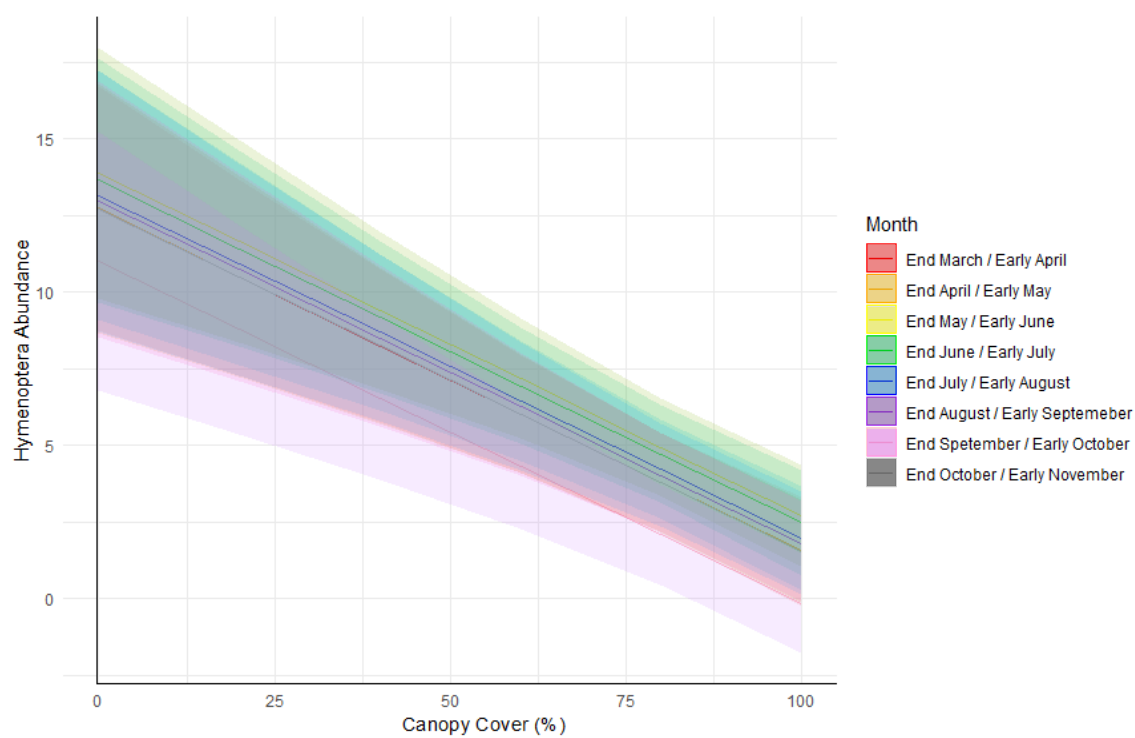


Figure 11. Predicted values ($\pm 95\%$ CI) for canopy cover in the top model for Hymenoptera abundance. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

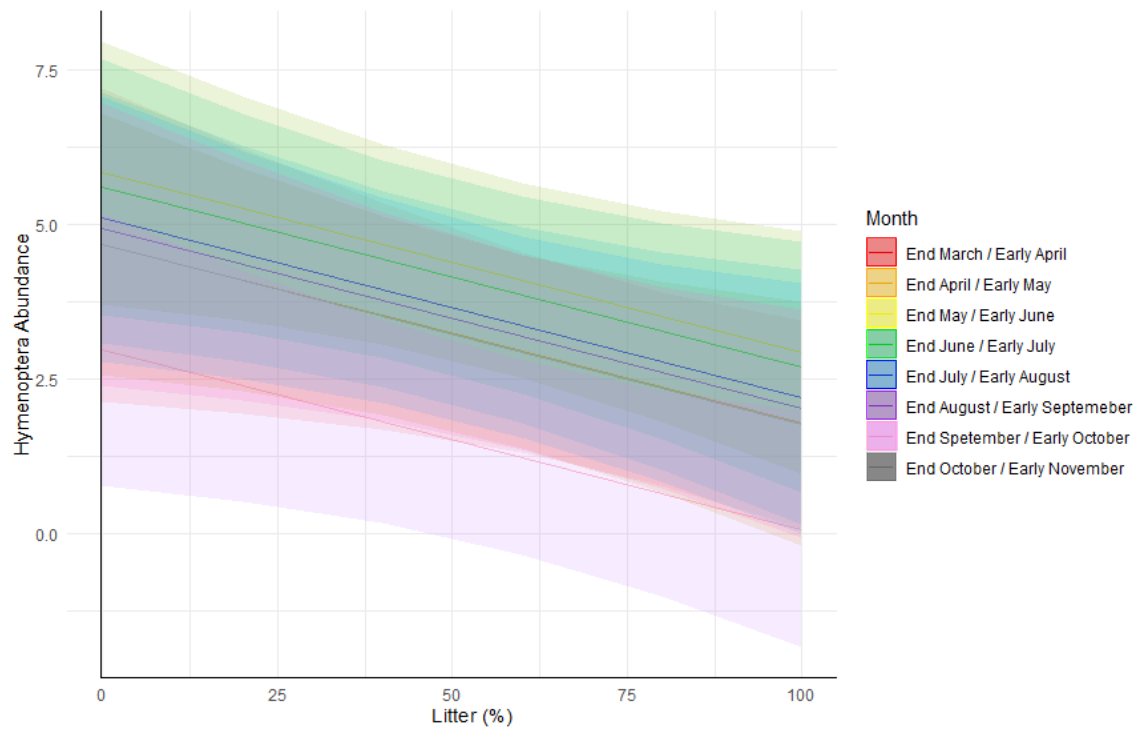


Figure 12. Predicted values ($\pm 95\%$ CI) for litter in the top model for Hymenoptera abundance. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

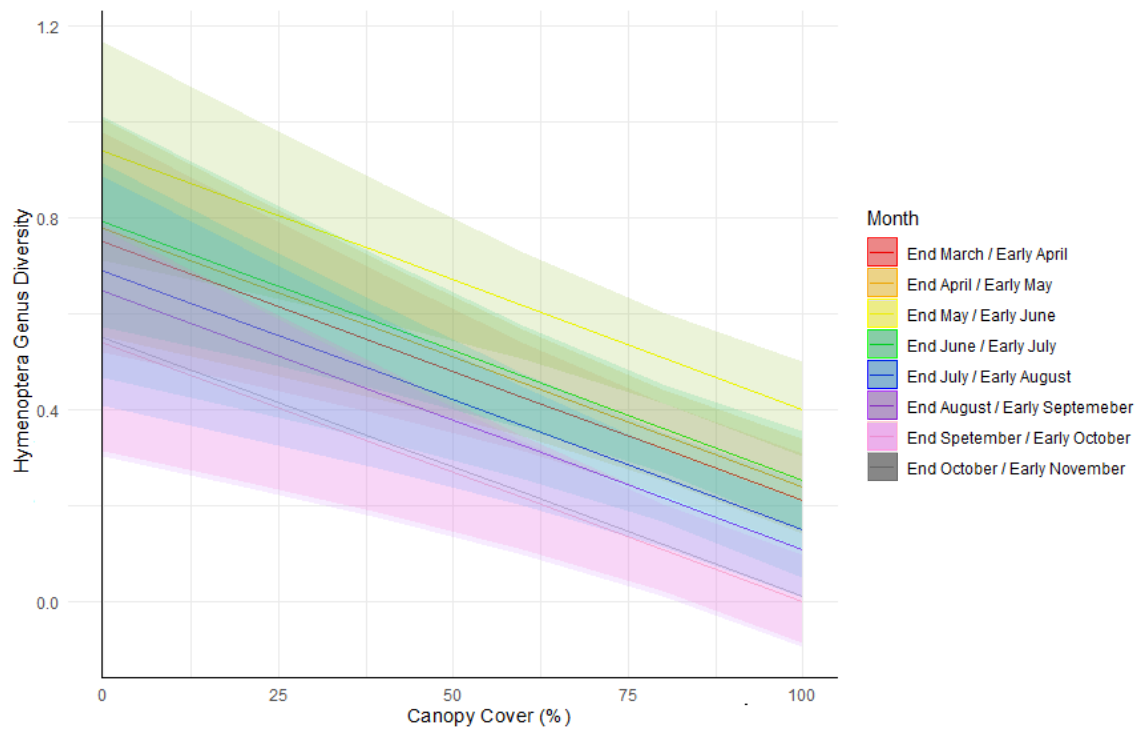


Figure 13. Predicted values ($\pm 95\%$ CI) for canopy cover in the top model for Hymenoptera genus diversity. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

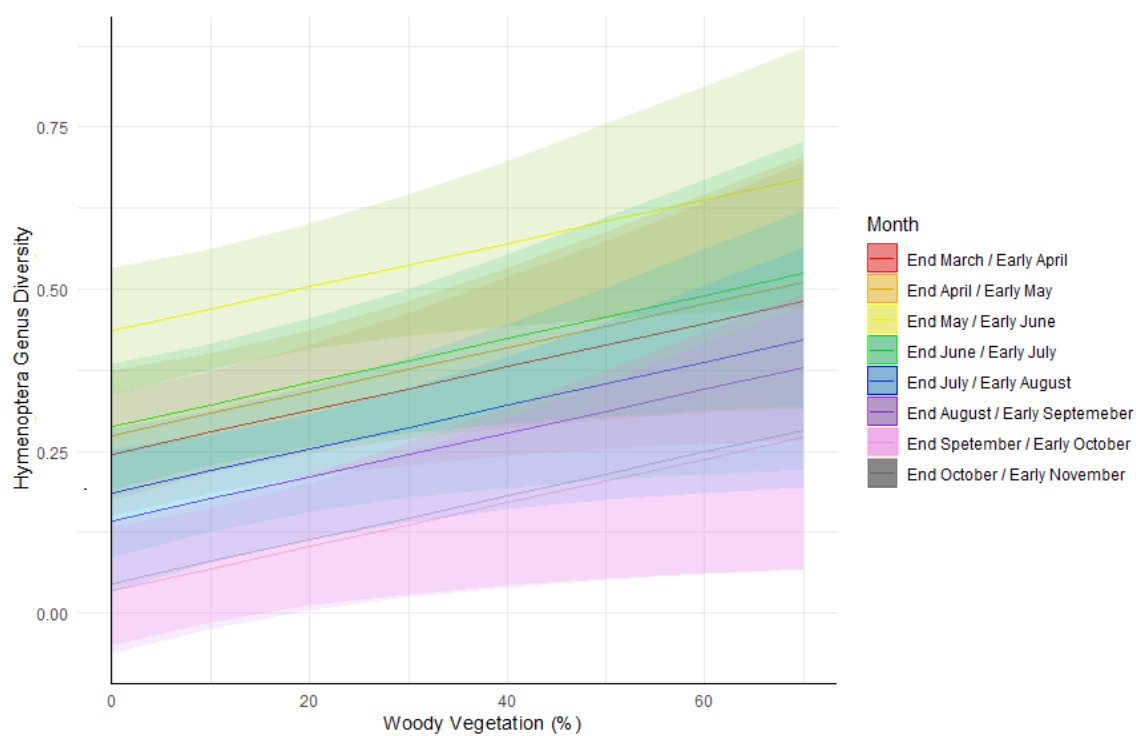


Figure 14. Predicted values ($\pm 95\%$ CI) for woody vegetation in the top model for Hymenoptera genus diversity. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

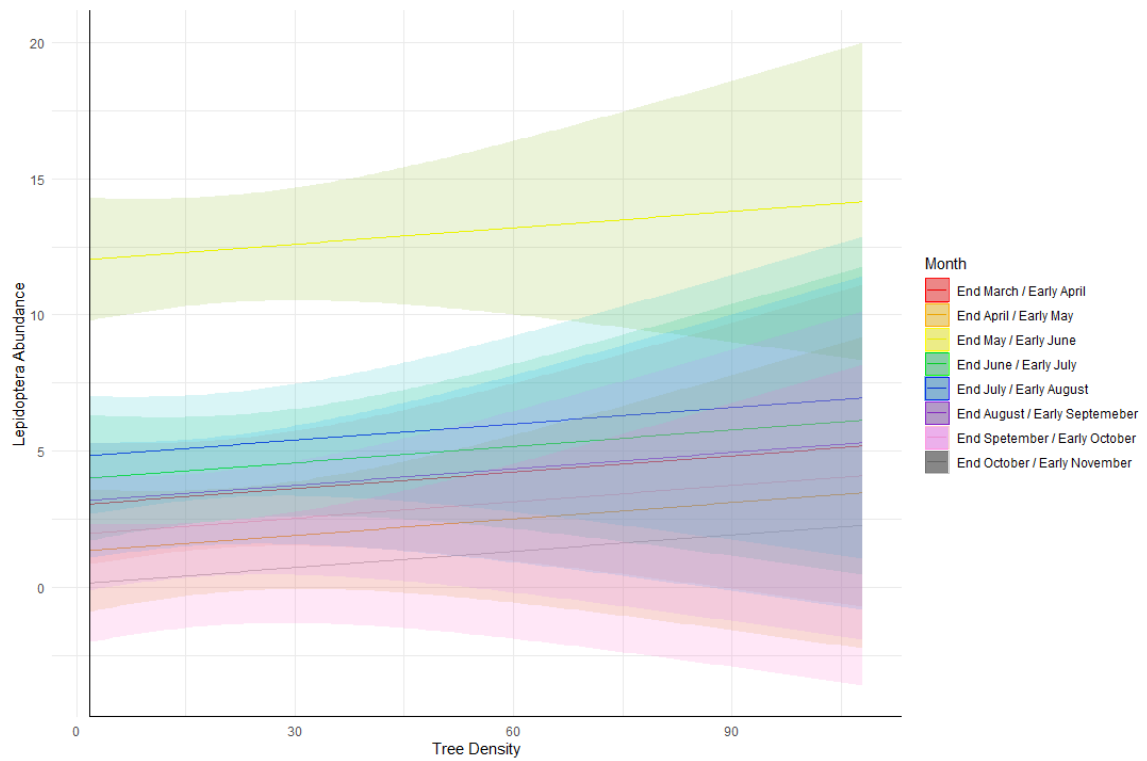


Figure 15. Predicted values ($\pm 95\%$ CI) for tree density in the top model for Lepidoptera abundance. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

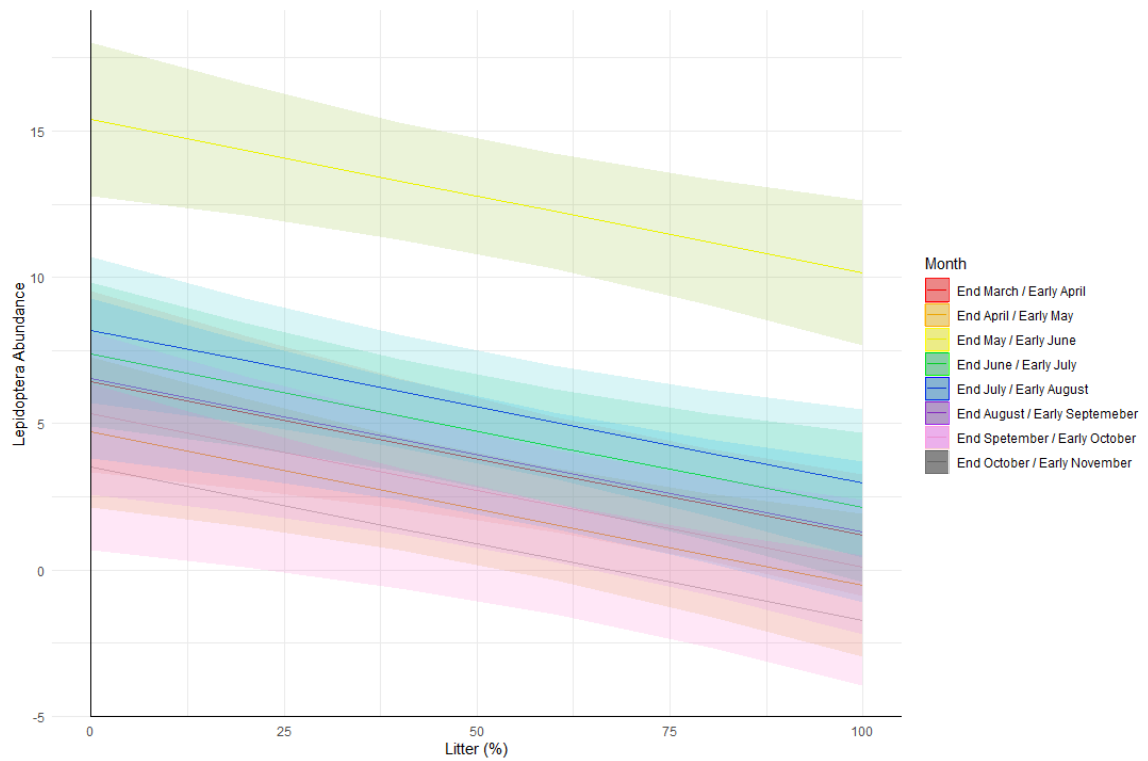


Figure 16. Predicted values ($\pm 95\%$ CI) for litter in the top model for Lepidoptera abundance. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

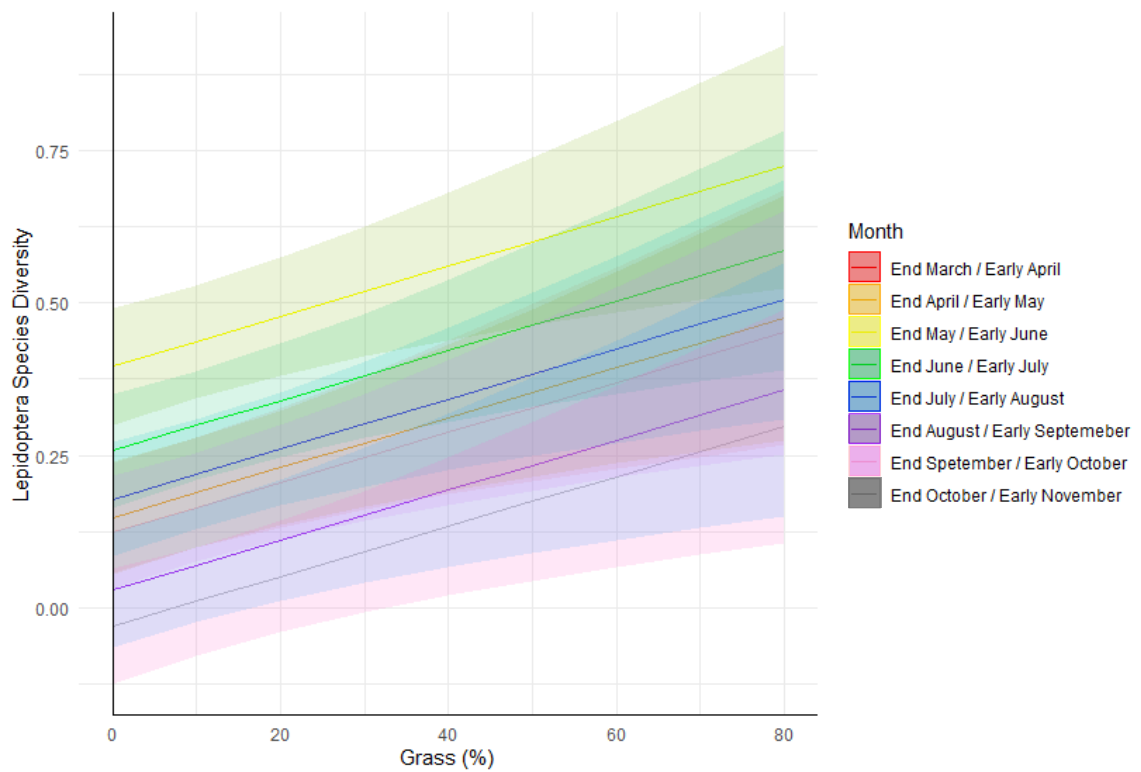


Figure 17. Predicted values ($\pm 95\%$ CI) for grass in the third ranked model ($\Delta AIC_c = 0.67$) for Lepidoptera species diversity. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

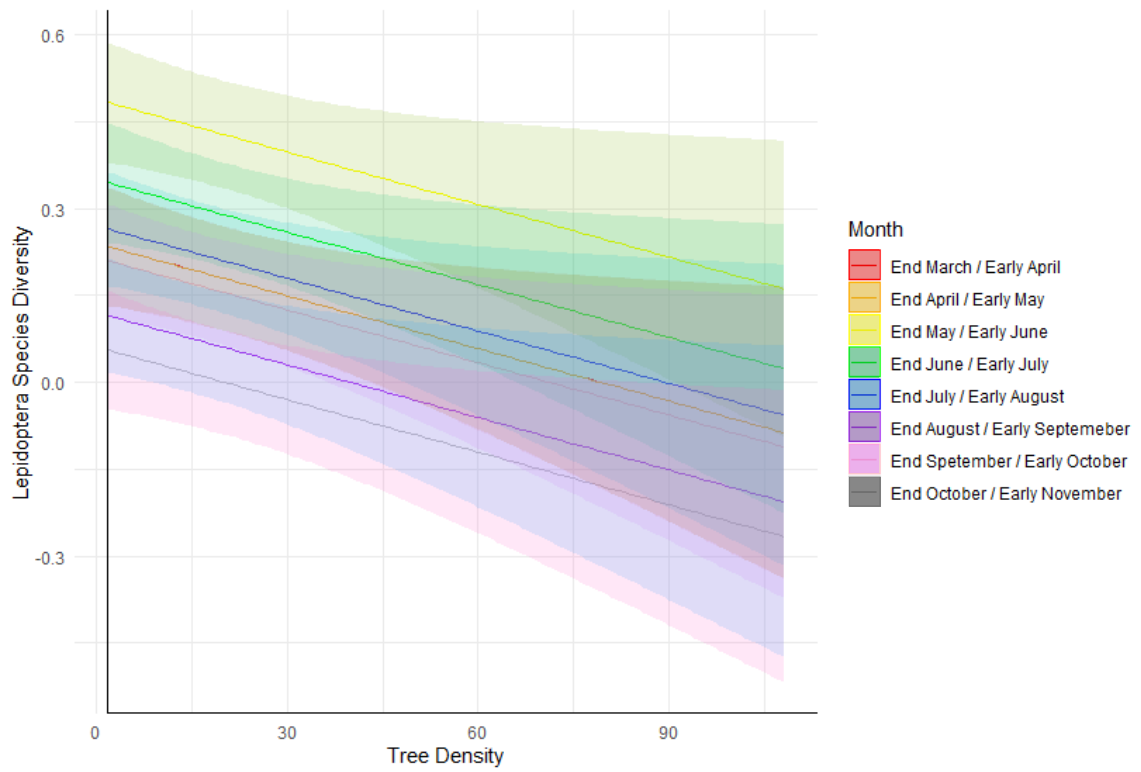


Figure 18. Predicted values ($\pm 95\%$ CI) for tree density in the third ranked model ($\Delta AIC_c = 0.67$) for Lepidoptera species diversity. Insects collected March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

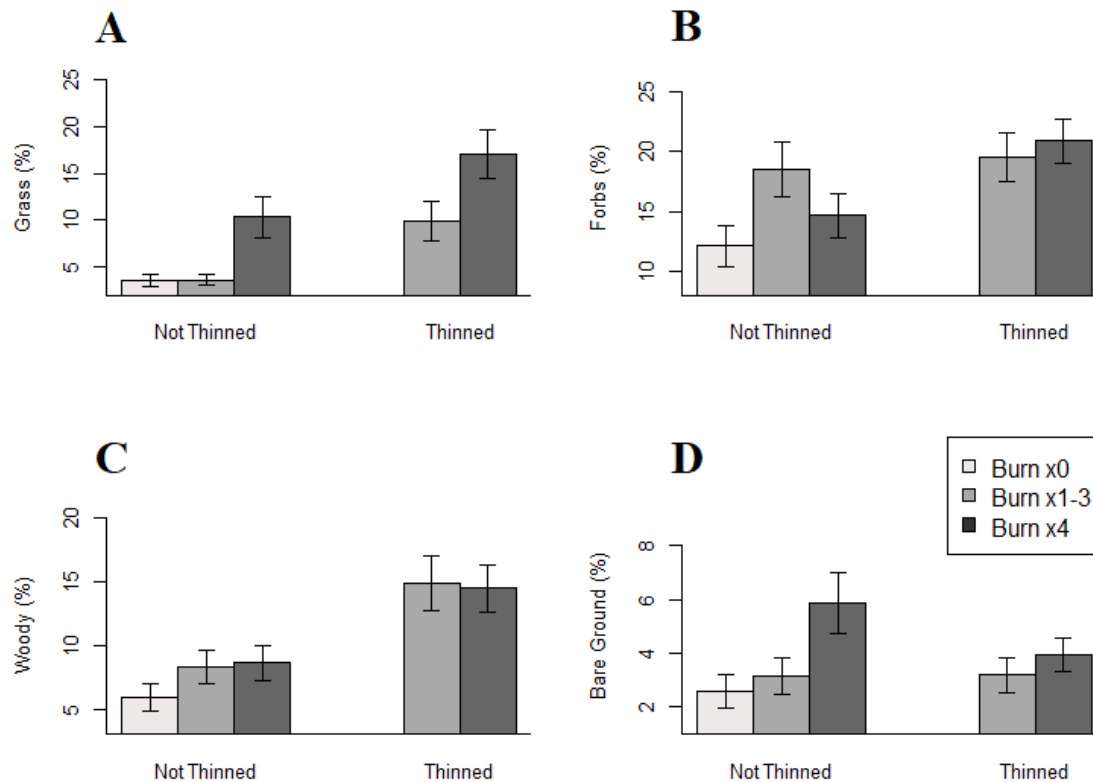


Figure 19. Mean percent ($\pm 95\%$ CI) grass (A), forbs (B), woody vegetation (C), and bare ground (D) per sampling point for each burn frequency and thinning status.

Pseudoreplication of the stands and seasonal differences in vegetation are not taken into account. Vegetation measurements taken March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

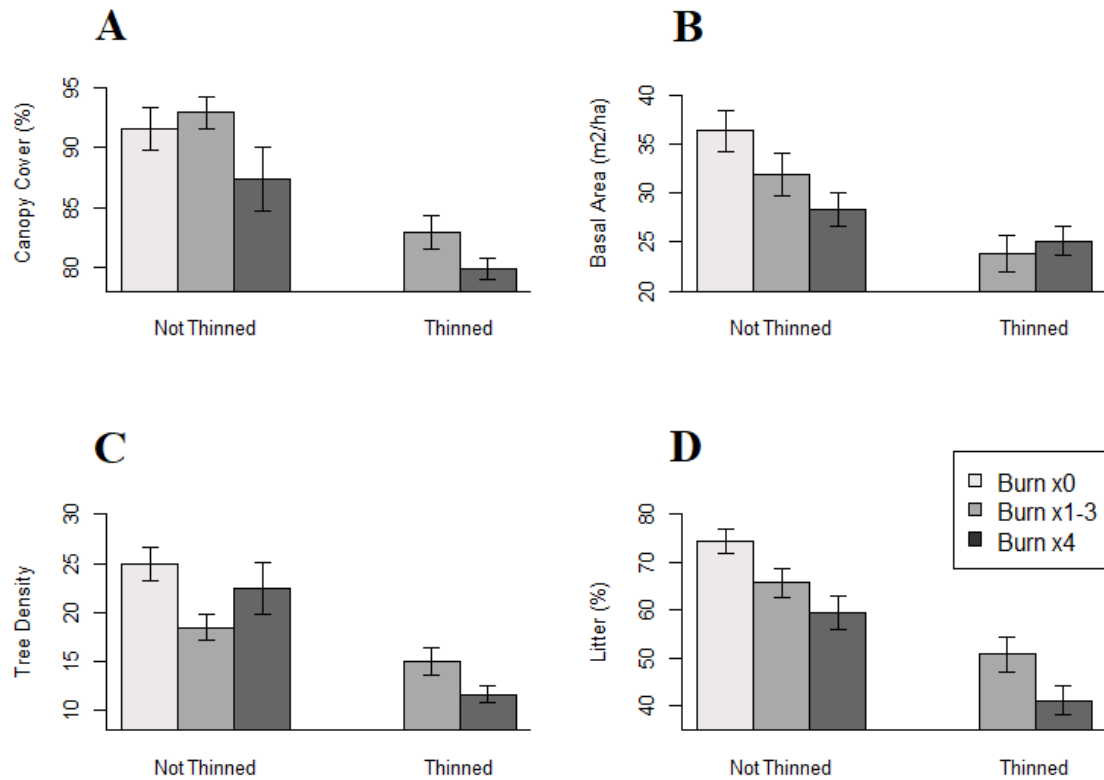


Figure 20. Mean ($\pm 95\%$ CI) canopy cover (**A**), basal area (**B**), tree density (**C**), and litter (**D**) per sampling point for each burn frequency and thinning status. Pseudoreplication of the stands is not taken into account. Vegetation measurements taken March–November 2019 in Johnson, Pope, Conway, and Van Buren Counties, Arkansas.

